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DISTRIBUTION OF FIDDLER CRABS IN GEORGIA SALT MARSHES[1]

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Introduction

The study of the distribution of animals in nature is especially interesting when several species of one genus occupy the same general area. Along the east coast of the United States there are three species of fiddler crabs of the genus *Uca* which live in the salt marshes. All three are found in the marshes surrounding Sapelo Island, Georgia, and this paper deals with experiments concerning their distribution in these marshes. I deal with the problem of why the crabs live in certain habitats within their range and not in others, not what determines or has determined their geographical range.

The three species of crabs are: *Uca minax,* the largest, generally associated with brackish water; *Uca pugilator,* commonly known as the sand fiddler crab, and *Uca pugnax,* found generally throughout the salt marsh.

Components of the environment which might be important in determining the distribution of these animals are substratum, food, salinity, exposure or tides, and other animals. The effects of these factors can be evaluated by answering the questions: What is the substratum choice of the animals when other factors are constant? Does the presence of other species of fiddler crabs affect this choice? Can the three species survive in all types of salt marsh or are they restricted to certain types? What are the salinity and temperature tolerances and salinity preferences of the species? What do the crabs feed on and how is this food distributed in the marsh?

Adult animals were used in most of the experiments. It is true that choice of area for settling by the megalops larvae is important in the distribution of the adults; nevertheless, adult fiddler crabs can and do move considerable distances over the marsh and could easily move to an environment different from that chosen by the larvae.

The Salt Marsh

The Georgia salt marshes occupy a band about eight kilometers wide, bordered by the land on one side and by the sea islands on the other. They are cut by a network of tidal rivers and creeks (Fig. 1).

The salt marsh may be divided into the following types determined by the organisms present (especially the species and forms of the vegetation), the particle sizes of the soil determined according to Bouyoucos (1937), and the elevation of the soil in relation to the tides. The main types starting from the tidal creeks and going toward the land are as follows: (Fig. 2)

The Creek Bank

Below the marsh vegetation there is a portion of the creek bank that is exposed by every low tide. The soil is extremely soft and the sand content varies from about 10 percent just below the vegetation up to 70 percent in some regions at the lowest levels that are exposed. In these regions large numbers of *Uca pugilator* are often found.

Tall Spartina Edge Marsh

In this type, limited to the banks of the creeks, the marsh grass, *Spartina alterniflora,* grows from one to three meters tall. (All of the *Spartina* in the marshes discussed here belongs to this one species.) The soil is very soft and the sand content is around 10 percent. No fiddler crabs inhabit this marsh type, but a square backed crab, *Sesarma reticulatum,* and a mud crab *Eurytium limosum,* are common. *S. cinereum* is also present.

Medium Spartina Levee Marsh

This is found on top of the natural levees that run alongside the creeks and on the side of the

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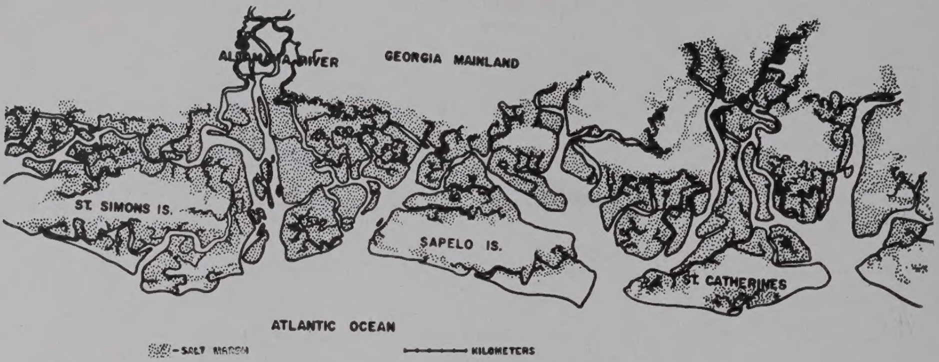

Fig. 1. Map of part of coastal Georgia showing salt marsh area between sea islands and mainland.

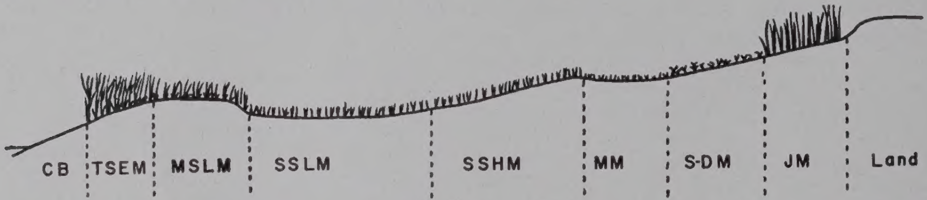

Fig. 2. Diagram of salt marsh types. CB = Creek Bank, TSEM = Tall Spartina Edge marsh, MSLM = Medium Spartina Levee marsh, SSLM = Short Spartina low marsh, SSHM = Short Spartina High marsh, MM = Minax marsh, S-DM = Salicornia-Distichlis marsh, JM = Juncus marsh.

levee away from the creek. The *Spartina* is about one meter tall. The soil is rather soft with a sand content of from 0 to 10 percent. On some of the higher levees the coverage of the grass may be sparse and the surface of the mud becomes dry and hard through exposure to the sun. *Uca pugnax* are found in this marsh along with two other crabs, *S. reticulatum* and *E. limosum*. In regions where the marsh is dissected to a great extent, the Tall and Medium Spartina marshes are the only types present.

Short Spartina Low Marsh

A large part of the salt marsh is of this type. It is found in areas between drainage creeks and is the lowest part of the vegetated marsh except for the Tall Spartina Edge marsh. The marsh grass is from 10 to 50 cm tall. The soil contains from 0 to 10 percent sand and is quite firm underfoot as a result of the network of *Spartina* roots. *Uca pugnax* is the only crab found in the sampled areas of this marsh except for *S. reticulatum* and *E. limosum* associated with mussel colonies (*Modiolus demissus*) where these occur.

Short Spartina High Marsh

This is a transition between the great extent of the marsh and the land. The *Spartina* is from 10 to 50 cm tall and the soil is firm as in the last type, but here the sand content of the soil runs from 40 to 70 percent. The elevation is greater than in the Short Spartina Low marsh. *Uca pugnax* lives in this region and *Uca pugilator* may often be seen feeding but apparently they do not burrow here to any appreciable extent.

Some relatively small areas near the land, which are slightly lower in elevation than their surroundings, have a very firm sandy-peaty soil, and are usually bordered by typical Short Spartina High marsh on the marshward side and by one or both of the succeeding types on the landward side. The sand content is about 30 percent and the plant covering of *Spartina* is very short, 10 to 20 cm tall. Because of the relative lowness of the area, water tends to remain on the surface where rains and evaporation cause the salinity to vary from 10 to 70 $^{0}/_{00}$. Since it is here that *Uca minax* is found most abundantly on the sea islands, this type of marsh will be referred to as *"Minax Marsh."* *U. pugnax* also occurs here.

Salicornia-Distichlis Marsh

This type occurs next to the land where the soil is 80 to 95 percent sand. *Spartina* occurs only as scattered and stunted plants and the ground is covered principally with species of *Salicornia* and *Distichlis spicata*. Parts of this region have no plant cover at all, existing as sand flats on which the surface temperature in summer may reach 45° C. This marsh is covered only at spring tides. *Uca pugilator* is the most abundant crab. *U. pugnax* occurs also. At the actual edge of the land *Sesarma cinereum* is usually abundant.

Juncus Marsh

This marsh is covered with the rush, *Juncus roemerianus.* It is usually on more elevated sites and places near fresh water and occurs in large expanses on the mainland side of the salt marshes near the river mouths. The soil is sandy and firm. The crabs include *U. pugilator, U. pugnax, U. minax,* and *S. cinereum.*

Population Samples

In order to determine the distribution of the crabs, samples of the populations in the marsh were taken by placing iron cylinders 1/5 m^2 in cross section over an area at high tide when the animals were in their burrows or at least not grouped together in herds. When the tide had ebbed the marsh enclosed in the ring was dug out by hand and the crabs separated, washed and weighed individually. Only crabs above 0.2 gm were sampled. This was the smallest size crab seen with egg masses. Smaller ones could not be adequately sampled by this method.

Table I shows the results of sampling during August and September, 1956. *Uca minax* was found only in the Minax marsh on the Sea Islands. No samples were taken near the river mouths on the mainland side of the marsh where this species also occurs. *Uca pugilator* burrowed in the creek banks and in the Salicornia-Distichlis marsh. Although *U. pugilator* was often seen feeding in the Short Spartina High marsh, apparently they do not burrow there. *Uca pugnax* is found in all types but the Edge marsh, but large numbers occur only in the Medium and Short Spartina marshes. The square-backed crab, *Sesarma reticulatum,* and the mud crab, *Eurytium limosum,* occurred principally in the Edge marsh where there were no fiddlers, and in the neighboring Medium Spartina marsh.

Feeding Experiments

Specimens of *Uca pugnax* and *U. pugilator* were kept in glass fingerbowls in the laboratory for one month and fed with a mixture of sand, clay, and either bacteria or fermented marsh grass. The bacteria were of species that occurred in the marsh. They were grown on nutrient agar at 30° C for two days, harvested with a rubber policeman, and mixed with the sand and clay to make a mud of the consistency of marsh mud. The marsh grass was finely chopped, mixed with seawater, inoculated with a little marsh mud, and then fermented for 10 days at 30° C. At the end of this period it was mixed in a Waring blender and combined with the sand and clay. There was not as much organic matter in this artificial mud as is found in actual marsh mud. Controls were fed the clay and sand moistened with aged seawater. Freshly collected animals were also used as controls. It was found that a *Uca* does not lose appreciable weight over considerable periods of starvation so that live weight changes could not be used as a criterion of food utilization. However, the ratio of organic matter to total dry weight does decrease during starvation and was used as the criterion of utilization of food. The data were subjected to analysis of covariance to test the significance of the means obtained.

The feeding tests showed definitely that *U. pugilator* and *U. pugnax* are able to live on bacteria or a mixture of bacteria and organic debris, i.e., the fermented grass mixture. The covariance analysis (Table II) indicates that the percent organic matter was significantly higher in experimentally fed crabs than in control, starved crabs ($P = 0.005$). There was no difference between the crabs fed on pure bacteria and those fed on the fermented mixture. Under the conditions of the experiment, *U. pugnax* individuals were most successful in maintaining their condition close to that of crabs freshly collected from the marsh (Normal) but in both species there was a significant difference between freshly collected crabs and those fed in the experiments. This probably resulted from experimental technique rather than any important deficiency in the food supplied.

Unfortunately, *U. minax* was not included in these experiments but it may be assumed that results would have been similar. They usually feed in the same manner as the other species (taking mud and sand into the buccal cavity, sorting the material with the mouth parts, passing part out at the posterior end of the cavity and retaining the remainder) although they also feed on large objects such as fish and crabs (Gray, 1942), and large males were observed on several occasions to catch, kill and eat members of the other two species of fiddler crabs. The other species ignore, for the most part, such materials as garbage and dead fish (Crane, 1941).

Contrary to the observations of Pearse (1936) and Gray (1942) all three species were frequently observed to feed under water, both in the marsh and laboratory. Adult *U. pugnax* often remain out of their holes and feed as the tide rises and

TABLE I. Population of adult crabs in various salt marsh types from Sapelo Island, Georgia, Aug.-Sept., 1956. Mean values per square meter are indicated. Parentheses enclose the 95% confidence limits of the mean

Species	Creek Bank	Tall Spartina Edge Marsh	Medium Spartina Levee Marsh	SHORT SPARTINA Low Marsh	SHORT SPARTINA High Marsh	Minax Marsh	Salicornia-Distichlis Marsh	Juncus Marsh
Uca minax	....	....	....	....	....	32(43-20)	....	?
Uca pugilator	52(71-33)	....	....	....	....	....	43(67-19)	?
Uca pugnax	13(21- 5)	....	61(73-48)	27(40-13)	18(28- 7)	4(7- 1)	12(22- 3)	?
Sesarma reticulatum	1(2- 0)	30(40-20)	21(30-13)	2(4- 0)	3(5- 0)	....	....	. .
Sesarma cinereum	....	1(2- 0)	....	....	....	2(6- 0)	?	?
Eurytium limosum	6(8- 4)	17(22-13)	4(6- 2)	....	....	....	....	. .

TABLE II. Covariance analysis of results of crab feeding experiments. Mean is percent organic matter

	Adjusted means	Variation source	Mean square	F	P
		Uca pugnax			
Control	43.8	Error	14.0	11.58	0.005
Fed crabs	49.7	Between means	162.6		
Normal	53.9	Error	15.6		
Fed crabs	50.0	Between means	194.2	12.4	0.005
Grass fed	48.5	Error	14.9		
Bacteria fed	51.0	Between means	14.8	no difference	
		Uca pugilator			
Control	39.5	Error	15.2		
Fed crabs	43.9	Between means	136.0	8.9	0.005
Normal	56.5	Error	14.5		
Fed crabs	44.3	Between means	138.9	9.6	0.005
Grass fed	44.4	Error	14.5		
Bacteria fed	44.9	Between means	4.8	no difference	

the same is less frequently observed in *U. minax*. The *U. pugilator* retire into their burrows with a rising tide, but may wander into tide pools and shallow creeks and feed under water at low tide.

TEMPERATURE TOLERANCE

Experiments to compare the survival of the three species of *Uca* at high temperatures were done by placing the animals in enough sea water of the desired temperature so that each animal was slightly more than half covered. The temperature which resulted in 50 percent mortality after one hour was found from the regression equation of temperature on mortality.

On the basis of seven determinations for each species the temperatures at which 50 percent of the animals died from the heat in one hour were: 39.9° C for *U. minax*, 39.5° *C* for *U. pugilator*, and 40.0° C for *U. pugnax*. There is no significant difference in these values and high temperature is therefore not important in determining the different distributions of the three fiddler crabs, although the crabs in the higher parts of the marsh encounter temperatures that are near the lethal level at times during the summer. Temperatures of 45° C on the open sand flats of the Salicornia-Distichlis marsh prevent *U. pugilator* from permanently occupying these areas, although they do feed there at night and in the cooler parts of the year.

SALINITY TOLERANCE

Fiddler crabs were placed in fingerbowls with water of 0, 7, 15, 30, 43, 49, and 58 $^{0}/_{00}$ salinity and survival noted. The water in each bowl was changed daily. Another series of fingerbowls was set up in which sea water of 30 $^{0}/_{00}$ salinity was alternated daily with fresh water.

It was only in the tests with 7 and 0 $^{0}/_{00}$ salinity that there were any differences in survival among the three species. At the higher salinities as well as in the experiment in which salinity was varied, all species survived more than three weeks, at which time these tests were discontinued. At 0 $^{0}/_{00}$ salinity, 50 percent of the *U. minax* had not yet died by the end of three weeks, 50 percent of the *U. pugilator* died after three and one-half days, while 50 percent of the *U. pugnax* died within one and one-half days. In water of 7 $^{0}/_{00}$ salinity, 50 percent mortality of the *U. pugnax* occurred after three days while more than 50 percent of both the other species survived the entire ten days of this test. These data are consistent with the general distribution of the animals. *Uca minax* is able to stand long immersion in fresh water and penetrate up streams and rivers. *U. pugilator* is less resistant but can survive soakings of the Salicornia marsh with rain water between spring tides, while *U. pugnax* can least stand dilution of its medium and is restricted to the tidal marsh.

SALT-FRESHWATER CHOICE

A wooden aquarium 120 cm long by 60 cm wide with a low partition down the center and mud or sand on the bottom was filled with freshwater on one side and water of about 30 $^{0}/_{00}$ salinity on the other. Crabs could move freely from one salinity to the other over the partition which prevented mixing of the waters. The salinities were checked periodically to see that no mixing or layering occurred. Crabs were placed in the aquarium and their position noted after 24 hours.

The results of this experiment are shown in Table III. Both males and females of *U. minax* showed a statistically significant preference for freshwater over salt. The males of *U. pugilator* and *U. pugnax* showed a significant preference for salt water over fresh. The females of these latter species were found more often in salt than freshwater but the differences were not statistically significant. It is likely, however, that there is a preference for salt water in females of *U. pugnax*. In all cases the preferences shown by the females were less strong than those shown by the males.

TABLE III. Percent of males and females of three species of fiddler crabs which prefer fresh or salt water in a 24 hour experiment. P is probability that results in row are not different

		Percent Preferring		
		Fresh water	Sea water	P
U. minax	male	68	32	0.001
	female	60	40	0.024
U. pugilator	male	40	60	0.02
	female	48	52	0.6
U. pugnax	male	20	80	0.001
	female	35	65	0.058

SUBSTRATUM PREFERENCE

Four aquaria, 75 cm by 35 cm, were set at an angle of 30 degrees from the horizontal. They were filled to half their depth, one with marsh mud, one with marsh sand, one with sand at the low end and mud at the high end, and the last with mud at the low end and sand at the high end. Sea water was put in each until it covered half of the substratum surface. Crabs were placed in the aquaria five or six at a time and after 24 hours the positions of the burrows which had been dug were recorded.

To test the substratum preference of the crab larvae, an aquarium was set up with the bottom covered with mud on one side and sand on the other in such a way that both substrata were under water at one end and above water at the other. Plankton from the water in the marsh creeks was placed in the tank and young crabs collected and identified as they appeared. Identification was made on the basis of the presence or absence of spoon-tipped setae on the merus of the second maxilliped (Crane, 1943).

Figure 3 diagrams the results of these tests. *Uca pugilator* burrowed almost exclusively in sand above water level. In those tanks that contained sand above water, almost 100 percent of the crabs made burrows but in the other tanks less than half did so. The crabs probably do not burrow in submerged sand because the burrow collapses about the animal as it digs.

U. minax showed a definite preference for mud whether it was above or under water. About half of the animals dug holes in the mud in those tanks with mud covering half of the bottom, while only one-quarter dug in the tank with an all mud substratum. This might indicate that these crabs prefer a mud in which there is a mixture of sand, or perhaps more likely, that they prefer an area of variable substrate.

The third species, *U. pugnax,* burrowed only in the mud and without any special reference to water level. (It is possible to make a successful burrow in submerged marsh mud because of its sticky consistency.) Forty percent of the crabs dug in the tank with an all mud bottom and 13 percent in those tanks with half the bottom covered with mud. In this species, as in the others, the crabs preferred to dig close to the sides of the tank.

The results of the larval and adult experiments were in accord. In all, 19 young crabs were found. Thirteen of these were *U. pugnax,* all of which burrowed on the mud side of the tank, and 6 were *U. pugilator,* of which 5 burrowed on the sand side and one on the mud side.

INTERFERENCE BY PRESENCE OF A SECOND SPECIES

The experiments described in the last section were repeated with two species present at one time and the percentage of each species that dug burrows noted. This was compared with the percent that dug burrows when the species was present in the aquaria alone and the results tested for significance in contingency tables (Table IV). The criterion of interference is not the relative number of holes dug by the two species present, but the number of holes dug by one species when alone compared with the number of holes dug by that same species when paired with another. This is a measure of the extent to which the added species can interfere with the behavior of the first. The relative number of holes dug by the two species is a measure of the extent to which the experimental situation approximated the habitats of the two species in the marsh and does not concern us

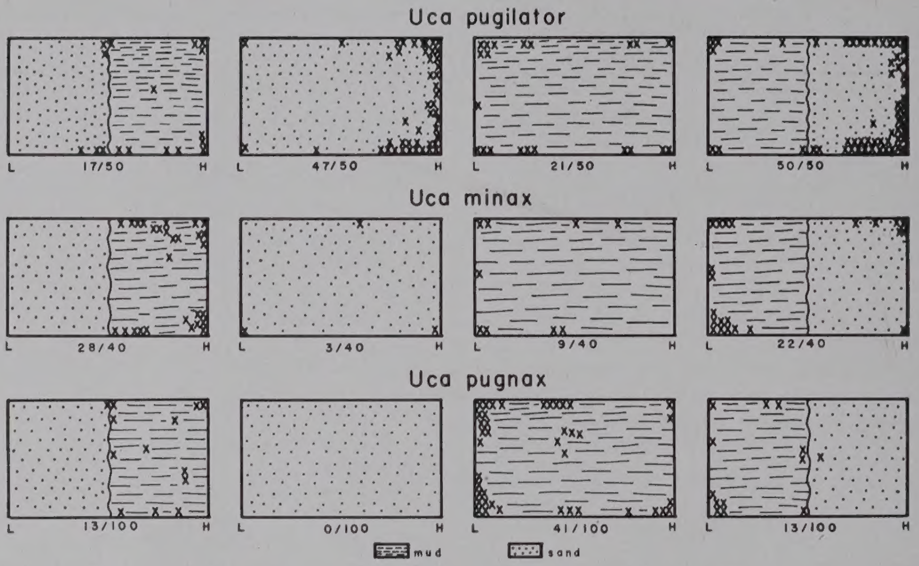

FIG. 3. Burrows dug by the three species of fiddler crabs in experimental tanks. Each x marks one hole. L—submerged half was under water, H—exposed half. Fraction is portion of animals that made burrows.

TABLE IV. Comparison of the percent of crabs that dug burrows in experimental tanks when each species was alone and when paired with each of the other two species. Percent is portion of animals that dug holes. Decimal is probability that value it follows is identical with value for that species when it was unpaired

Species Combinations	Mud exposed Sand submerged		Sand exposed Sand submerged		Mud exposed Mud submerged		Sand exposed Mud submerged	
U. pugilator								
alone	34%		94%		42%		100%	
with pugnax	35%		22%	0.001†	35%		28%	0.001†
with minax	25%	0.5	38%	0.001†	28%	0.22	48%	0.001†
U. minax								
alone	70%		8%		23%		55%	
with pugilator	37%	0.02*	5%		17%		17%	0.008†
with pugnax	16%	0.001†	5%		23%		17%	0.001†
U. pugnax								
alone	13%		0%		41%		13%	
with pugilator	11%		0%		27%	0.76	13%	
with minax	21%	0.15	0%		38%		22%	0.12

*Significant †Highly Significant.

here since with each species at least one tank approximated their habitat closely enough to get a large number of burrows.

When *U. pugilator* was tested with either of the other species there was a reduction of 50 percent or more in the number of burrows that it dug in the sand above water. The reduction was greater with *U. pugnax* than with *U. minax* as the paired species. In those tanks where there was no sand above water and *U. pugilator* was forced to burrow in an unfavorable substratum, its behavior was not changed by the presence of another species.

When *U. minax* was paired with either of the other species, there was a significant reduction of from 25 percent to 55 percent in the number of burrows in the tanks in which the bottom was half covered with mud, the tanks in which the highest portion of *U. minax* burrowed when they were tested alone. The greatest reduction again resulted from the pairing with *U. pugnax*.

The presence of a second species in the tanks caused no significant change in the behavior of *U. pugnax*.

SURVIVAL IN THE MARSH

Cages 60 cm square, open at the bottom and with a removable cover, were built of ¼ inch

TABLE V. Comparisons of survival between pairs of species of fiddler crabs tested during 2 week intervals in different marsh types around Sapelo Island, Georgia. The fractions represent the portion surviving, the decimal is the probability that the fractions are not actually different

	Short Spartina Low Marsh	Medium Spartina Marsh	Short Spartina High Marsh	Salicornia-Distichlis Marsh	Creek Bank	Minax Marsh
U. minax	6/10	5/9	7/10	0/10	12/16	18/22
vs.	0.003†	0.4	0.11	0.11	0.2	0.2
U. pugilator	0/12	4/10	10/10	3/10	15/16	16/24
U. minax	9/16	5/9	7/20	....	8/10	21/22
vs.	0.7	0.6	$\sim$1	....	0.5	0.013*
U. pugnax	5/18	6/10	8/22	....	9/10	15/23
U pugilator	39/202	8/16	36/52	7/32	16/17	13/17
vs.	<0.001†	0.8	0.6	0.02*	1.0	0.3
U. pugnax	147/215	12/16	40/54	1/33	16/17	10/16

*Significant. †Highly significant.

hardware cloth reinforced with wood. These were sunk 30 cm into the marsh until the hardware cloth was deep enough that the crabs would not dig under it. Marked crabs were placed in the cages set out in various types of marsh and their survival after two weeks, one semi-lunar cycle of tides, was found.

Comparisons of the survival of the three species with each of the others are shown in Table V. Comparisons, not simple percents of survival, were used since weather conditions during the test intervals were not identical. The tests were made both with the species in neighboring cages and with two species in one cage. Survival was the same in both cases for each species and the results are combined in the table.

U. pugilator did not survive in the Short Spartina Low marsh, the most common type, while *U. minax* and *U. pugnax* did about equally well. The comparisons between *U. pugilator* and *U. pugnax* in this marsh type were repeated several times and were made with crabs of 0.1 gm size as well as with 1-3 gm animals; results were the same in all tests and have been combined in the table. The reason for the high mortality of *U. pugilator* is not known. It could not have been from starvation since the crabs had survived in the laboratory under similar temperature conditions for three times as long. It is possible that the lack of sand in the substratum is the important factor. Crane (1943) points out that the species of *Uca* that are associated with sandy environments have numerous spoon-shaped setae on the merus of their second maxilliped and that seate of this type are lacking or are fewer on species that live in mud. These spoon-shaped setae, in *U. pugilator* at least, are also very numerous on the protopodite of the first maxilliped. Although the exact function of these setae is unknown, they are presumably useful in the sorting process that goes on in the buccal cavity during feeding. Perhaps the presence of these spoon-shaped setae, and hence the absence of the regular feather-like setae, in some way prevents the crabs from living where there is no sand in the substratum.

In the Salicornia-Distichlis marsh, *U. pugnax* and possibly *U. minax,* survived less well than *U. pugilator*. The extreme conditions of heat and dryness during the neap tide interval account for the low survival in the experiments of all species in this marsh type. Normally, in this unfavorable period, the crabs move at night to moist portions of the marsh to feed but the animals confined in the cages could not obtain this relief.

In the Minax marsh fewer *U. pugnax* survived than *U. minax*. All of the other areas, the Medium Spartina Levee marsh, the Short Spartina High marsh, and the Creek Bank, were equally favorable to all three species. Survival of *U. pugilator* in the Medium marsh was probably helped by the use of a high place on the levee as a test area where the soil was somewhat drier and firmer than in other Medium marshes.

DISCUSSION

It seems doubtful that food is a factor in the distribution of the fiddler crabs. They can all feed on the algae, bacteria, and partly decomposed marsh grass that is found in the mud and sand of the marsh. While there are probably not enough bacteria to support the crabs, these microorganisms may supply important nutrients (Burkholder, 1956; Burkholder and Burnside, 1957) and the fact that crabs can utilize objects as small as bacteria argues for their being able to use much of the organic material in the marsh soil.

Only in the high sand flats might this food be in short supply and the crabs do not live in these areas, partly because of the high temperatures encountered there, although they do feed on these sand flats when these are moistened by rain or spring tides. In other parts of the marsh there is more organic material than all the organisms together can use as shown by the accumulation of mud rich in organic matter.

The possible effect of predation on the distribution of these crabs was not tested in any way but may be evaluated from general observations. Racoons and Clapper Rails feed regularly on fiddlers but probably do not have any effect on their distribution since these predators do not prefer any species of fiddler over the others and feed throughout the marsh. Aquatic predators of possible importance include fish, mud crabs, and blue crabs. These latter animals feed under water and their predation is thus concentrated on the creek banks which are under water more of the time than any other part of the fiddler's habitat.

Predation and the other factors will now be considered as they affect each of the three species.

Uca pugnax.

The distribution of this species in the salt marshes is considered to be conditioned principally by its preference for a substratum composed largely of mud. Also it prefers to burrow where there is vegetational cover (Schwartz and Safir, 1915). For these reasons it is found in the Medium and Short Spartina marshes. The *U. pugnax* move down through the Edge marsh to feed on the creek banks. They do not remain there in large numbers because of the lack of vegetation and they avoid burrowing in the Edge marsh for some other reason. Predation by aquatic predators is probably important in limiting their distribution at these lower levels. The *U. pugnax* frequently remain outside their burrows when the tide rises while *U. pugilator* almost never does and the former are therefore more subject to predation by aquatic animals. On the land side of the marsh, the distribution of *pugnax* is probably determined by substratum preference, at least in those areas where there is a sandy Salicornia-Distichlis marsh. Where the Short Spartina marshes abut directly on the land *U. pugnax* is limited by the dryness and low salinity of the land. Competition with other species of fiddlers does not seem to be of importance in any part of their distribution in the Georgia marshes.

Uca minax.

The distribution of this species is determined both by its preference for muddy substratum and brackish water and by competition with other species of fiddler crabs for space to make burrows. The preferences would account for this crab being found only in the muddy areas near the land where flooding with fresh water occurs. Its high relative tolerance of fresh water enables it to survive in areas where the other two species could not. Since *U. minax* survives perfectly well in the Short Spartina marshes, the distribution in that direction may be limited by interference with burrowing by *U. pugnax*. Both interference by *U. pugilator*, which is less effective than interference by *U. pugnax*, and lessened ability to survive, restrict the distribution of *U. minax* toward the high sandy marsh.

Uca pugilator.

The distribution of the third species is limited by competition or interference in burrowing, by substratum preference, and by inability to survive in certain marsh types. It is found only where there is appreciable sand in the substratum, usually more than 40 percent, but it may be found in places on the creek banks where the sand content is as low as 10 percent. In these latter situations, however, the sand content increases down the bank from 10 percent at the top to 60-70 percent at the low tide level. The crabs feed at the lower levels but are forced to live at the upper edge since the lower levels are exposed only a short time at each low tide. They are stopped at the upper edge of the creek banks by the muddy substratum of the Edge marsh. *U. pugilator* can survive in the Medium Spartina marsh but avoids it because of the lack of sand. The *U. pugilator* of the Salicornia-Distichlis marsh are probably restricted by interference from *U. minax* and especially *U. pugnax*. *U. pugilator* ranges into both the Minax marsh and the Short Spartina High marsh while feeding but since these crabs almost always return to their burrows or dig new ones before the tide rises, and since they are presumably prevented from burrowing in these two adjacent marsh types by the presence of the other fiddler species, they are effectively limited to the high marsh where the other species do not occur.

The evidence for competition between the species of fiddlers is not as complete as it might be. To remove, for example, *U. pugnax* from the Low Spartina High marsh and see whether or not *U. pugilator* would then colonize that marsh would be an experiment preferable to the one done in the laboratory where the two species were artificially confined together. But the field experiment is impractical because of the great labor involved and laboratory tests must suffice. The conclusion that competition is effective is strengthened by the survival tests which show that species can live in marshes where they do not, and by the observation that *U. pugilator* does feed in the region in which we suppose competition prevents burrowing. These tests and observations prove that the species are at least potential competitors in nature.

It may be concluded that food is unimportant in determining the distributions of the three species of fiddler crabs. Substratum preference, salinity tolerance and preference, predation, and competition (in the sense that the presence of one species in an area interferes with the use of that area by another species) are all important to some extent. Salinity and substratum preferences are important for all three species while interspecific competition is important only to *Uca pugilator*.

SUMMARY

Factors controlling the distribution of the fiddler crabs, *Uca minax, U. pugilator,* and *U. pugnax,* were studied in the Georgia salt marshes. The salt marsh is described and divided into types: Tall Spartina Edge marsh, Medium Spartina Levee marsh, Short Spartina Low marsh, Short Spartina High marsh, Salicornia-Distichlis marsh, and Juncus marsh. Sampling showed that *U. minax* is found in certain parts of the Short Spartina High marsh and Minax marsh; *U. pugilator* is found on the tidal creek banks and in the Salicornia-Distichlis marsh; *U. pugnax* is found in all but the Edge marsh but is numerous only in the Medium and Short Spartina marshes.

Feeding experiments showed that the crabs could live on bacteria or fermented marsh grass mixed with mud or sand. This sort of food is widely distributed in the marsh and is not therefore a factor in crab distribution.

The lethal high temperatures for the three species are nearly the same and are not a factor in their distribution.

U. minax could live in fresh water for more than three weeks, *U. pugilator* for a few days, *U. pugnax* for only one and one half days. When offered fresh and salt water *U. minax* chose to live in fresh; the other two species chose salt.

Substratum preference tests showed that *U. minax* and *U. pugnax* preferred mud either above or under water. *U. pugilator* preferred sand above water. When another species was present, the number of burrows dug under favorable conditions by *U. pugilator* was reduced by 50 percent or more. A second species caused a similar reduction of over 25 percent for *U. minax* but no significant reduction for *U. pugnax*.

U. pugilator was unable to survive in the marsh types with a pure mud substratum, a result possibly correlated with special setae on the maxillipeds. In the Sailcornia-Distichlis marsh, *U. pugilator* survived better than the other species.

It is concluded that the distribution of *U. pugnax* is determined by preference for vegetated muddy substratum and salt water; predation may limit it toward low tide level. *U. minax* chooses sites with mud substratum and fresher water; competition may be of some importance in limiting its spread into other marsh types. *U. pugilator* chooses sandy areas but is prevented from occupying all the sandy marshes by competition with the other two species.

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THE DETERMINATION OF CHOLINESTERASE IN THE BRAIN TISSUE OF THREE SPECIES OF FRESH WATER FISH AND ITS INACTIVATION IN VIVO

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The cholinesterase activity of the tissues of animals, vertebrates and invertebrates, has been studied extensively with particular reference to the physiological significance of the acetylcholine-cholinesterase system and the transmission of nerve impulses. These investigations have been reviewed by Augustinsson (1948). With the introduction of organic phosphorus insecticides and establishment of the inhibition of cholinesterase activity by these compounds (Mazur and Bodansky, 1946), new lines of investigation on the action of these and related compounds were opened (Chadwick and Hill, 1947; Koelle and Gilman, 1949; Dubois, Doull and Coon, 1950; Chamberlain and Hoskins, 1951; Frawley *et al.,* 1952; and Hartley and Brown, 1955).

The extensive use of organic phosphorus insecticides with potential hazard to both wildlife (Young and Nicholson, 1951) and man (Brown and Bush, 1950; Grob, 1950) and the development of anticholinesterase compounds, nerve gases, with potential military application (Wood, 1950) requires a broader knowledge of the behavior of these compounds in many ecological situations. One of these is the possibility of contamination of natural waters with anticholinesterase materials to the extent that a hazard to aquatic life may develop. The studies to be reported in this paper will describe the normal cholinesterase activity of fish brain tissue and the change in activity on exposure to anticholinesterase materials.

Methods and Materials

Three species of fresh water fish were used in this study, the fathead minnow, *Pimephales promelas;* the green sunfish, *Lepomis cyanellus;* and the goldfish, *Carassius auratus.* The fish were obtained from hatcheries in Maryland and West Virginia. New supplies of fish were obtained monthly so that the fish material was seldom kept in the laboratory tanks longer than one month.

The brain of the fish was selected for assay of cholinesterase (ChE) since it provided a relatively large amount of the specific ChE in a readily accessible tissue (Mendel and Rudney, 1943; Augustinsson, 1948). The fish brains were secured by cutting off the top of the skull and snipping the brain loose at the optic nerves and base of the medulla. This permitted lifting the brain free of the skull. The wet weights of the brains were detemined by weighing on small pieces of tared aluminum foil.

The weighed brain was then transferred to a tissue homogenizer and a brei prepared in 2-3 ml of buffer solution of the following composition: 0.2M $NaCl$, 0.02M $MgCl_2$, 0.194M K_2HPO_4 and 0.006M KH_2PO_4 with the pH adjusted to 8.2.

After draining and rinsing from the homogenizer, the brei was diluted with additional buffer to contain approximately 1-4 mg of brain tissue per ml of solution. The dilution enabled the assay to be restricted to the region of optimum accuracy of the assay method described below.

One milliliter of the diluted brain brei was pipetted into a test tube and incubated for 20 minutes at 25°C with one ml of 0.004M acetylcholine chloride (Merck) (ACh) prepared in 0.001M sodium acetate of pH 4.5. The residual ACh was then determined by reaction with alkaline hydroxylamine (Hestrin, 1949) and the color developed read on a Klett-Summerson photometer. A duplicate tube containing all reacting materials, but in which the acid was added prior to the alkaline hydroxylamine, was used as a control for turbidity and color. The ChE activity of the brain brei is reported in terms of micromoles ACh split per mg brain per hour.

In some instances aliquots of the brain brei were assayed for brain protein using the Folin phenol reagent (Lowry *et al.* 1951). The ChE activity in these cases was reported in terms of micromoles ACh split per hour per mg of brain protein. A standard protein curve was prepared using dried egg albumin. This procedure appeared justified by the fact that the amount of tyrosine and tryptophan in egg albumin is of the same order of magnitude as in fish brain protein (Block and Bolling, 1951). The relationship between fish brain weight and brain protein is shown in Figure 1.

The anti-ChE materials used in this study were isopropyl methylphosphonofluoridate (Sarin) and

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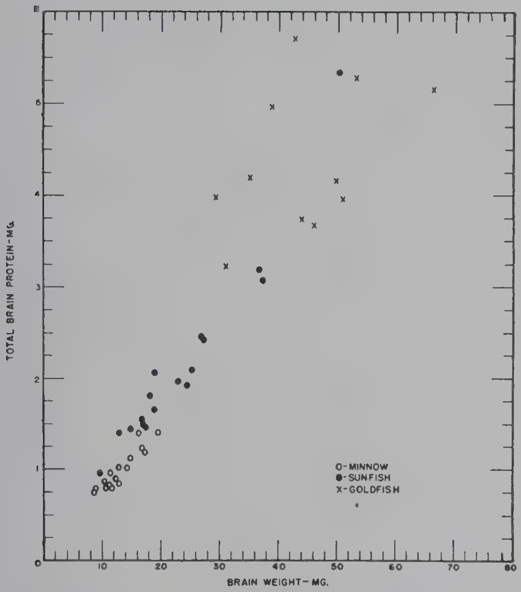

Fig. 1. The relationship of total brain weight to brain protein as determined with the Folin phenol reagent.

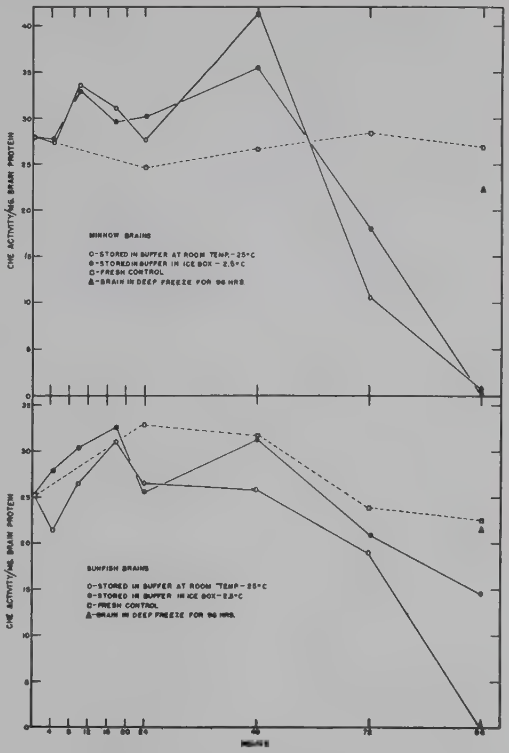

Fig. 2. The change in cholinesterase activity of whole brains at various time intervals following removal from the fish and under different conditions of storage.

cyclohexyl methylphosphonofluoridate. The compounds were prepared in other laboratories of the Chemical Corps. Aqueous dilutions were prepared from weighed samples.

To facilitate handling of the fish brain material a study was made to determine what changes in fish brain ChE activity occurred upon storage following death. The changes were determined using minnow and goldfish brains. A sufficient number of brains of each species were removed and stored so that at least two or three brains of each were available for assay at the various time intervals. Whole brains, in a small quantity of buffer, were stored at room temperature (25°C ± 1.0). Another set of brains in buffer solution was placed in a refrigerator at a temperature of about 2.5°C and a third set of brains was placed in a deep freeze at —35° to —40°C. The last set was assayed at the end of the experiment only. Each time a ChE assay was made, fresh brains from fish in the stock tanks were used as controls. The stored brains were not homogenized until assayed.

The ChE activities for the stored and control brains, over a period of 96 hours, are reported in Figure 2 in terms of activity per milligrams of brain protein. Each point represents an average of 2 or 3 brains assayed. In comparison with the control values, the minnow brain ChE activity shows a rise for 48 hours in both the brains stored at room temperature and those in the refrigerator, followed by a very marked and precipitous decrease to practically zero at 96 hours. The sample stored in the deep freeze shows an activity which is slightly lower than the fresh control at 96 hours but not outside the expected limits of significance.

The ChE activity of sunfish brains changes in a similar fashion on storage. However, in the first 48 hours the change in the activity is somewhat similar to that of the control brains. The reduction in brain activity appears to start at 24 hours and shows a decrease by 96 hours which is proportional to the storage temperature. The activity of brains at room temperature has decreased to practically zero, that at 2.5°C has decreased in activity by 35 percent, whereas the brains stored in the deep freeze for 96 hours have essentially the same activity as the control.

These changes in fish brain ChE activity are probably due to autolysis and bacterial action. However, it is evident that storage of brain material up to 96 hours is possible in a deep freeze.

Results

In the experiments to be described an attempt will be made to answer these questions about the fish brain ChE activity: (1) What is the normal ChE activity of the brain of these three species? (2) What happens to the brain ChE activity when the fish is exposed to anti-ChE materials?

The normal ChE activity of the brain tissue of the three species of fish investigated shows a proportionality between total activity of the individual brain (micromoles ACh split per hour by the entire brain) and the brain weight (Figure 3). The larger brains, as might be expected, have larger quantities of ChE. However, the specific activity, i.e., activity on a unit weight basis, for a series of brains extending over a fairly wide range of brain sizes, decreases as the brain size increases (Figure 4).

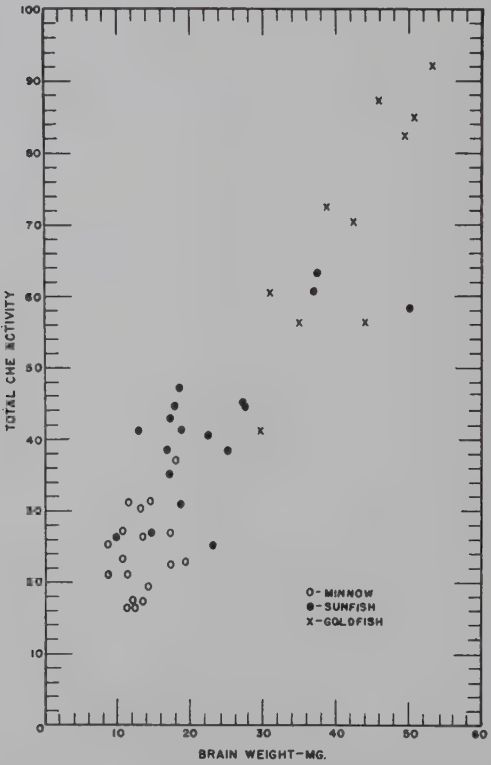

Fig. 3. The total cholinesterase activity in individual fish brains as related to total brain weight.

The exposure of fish to anticholinesterase substances depresses the level of brain ChE activity. When death of the fish takes place the level of ChE activity has fallen to about 30-60 percent of normal activity. If exposed fish are placed in fresh water the ChE activity of the brain returns, over a period of time, to normal level. The reduction in activity and return to normal levels is shown in Figure 5. The fish in these experiments were exposed to cyclohexyl methylphosphonofluoridate for 24 hours. At the end of the exposure the survivors were placed in fresh water to allow for recovery. A total of 40 fish of each species was exposed in batches of 10 per 15 liter aquaria. Their response to the anticholinesterase material is shown in Table I.

Table I. Response of fish on exposure to cyclohexyl methylphosphonofluoridate

Fish	Exposure concentration parts per billion	No. dying per total exposed 24-hour response	% of initial ChE activity of survivors after 24 hours exposure
Sunfish. . . .	0.6	3/40(7.5%)	49.5
Minnow. . .	1.1	16/40(40%)	31.7
Goldfish. . .	2.0	4/40(10%)	28.8

Surviving fish were then assayed at various time intervals until their brain ChE activity approached or attained the range of the control fish. This recovery period extended upward of two weeks and, in the case of the goldfish, recovery to levels of control fish brain activity was not attained in the course of the experiment. The fluctuation of control activity probably represents the degree of variation that can be expected from the material and assay.

The pattern of recovery of ChE activity of brain and other tissues has been determined in other species. Hunt and Riker (1947) have observed that cats injected with di-isopropyl phosphorofluoridate (DFP) showed a regeneration of muscle ChE that is complete in two weeks but brain ChE only reached a level 69 percent of normal after one month. In a comparison of six organic phosphorus compounds used in therapy and agriculture, Frawley *et al.* (1952) found that the brain ChE activity of rats, given these compounds by stomach tube, returned to normal values at times varying from 72 hours for octamethyl pyrophosphoramide (OMPA) to more than 4 weeks for DFP.

The significance of reduced ChE activity as a measure of sensitivity to anti-ChE materials can be seen in the following experiment. One hundred twenty minnows in 12 batches of 10 per 15 liter aquaria were exposed to 2.5 ppb (concentration, by weight, of 2.5 x 10^{-9}) of Sarin for 24 hours. Following the initial exposure, the survivors were placed in fresh water and at subsequent intervals exposed in 5 batches of 10 each

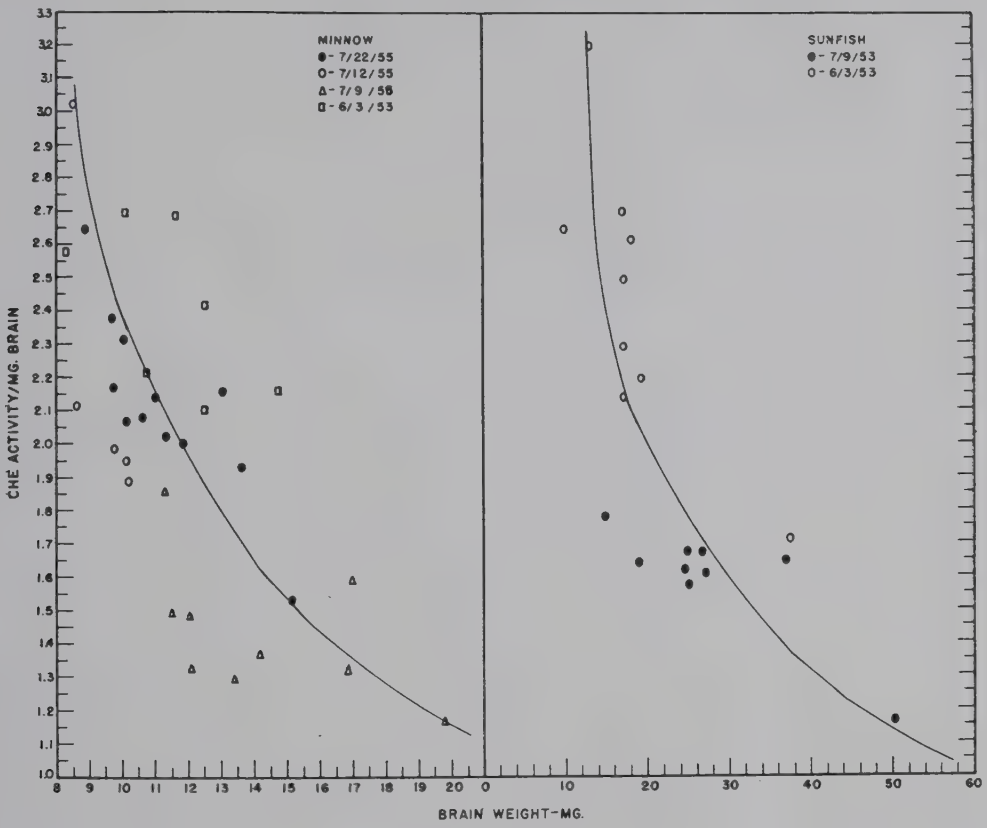

FIG. 4. The cholinesterase activity per milligram of brain as related to total brain weight. The dates represent the various sets of determinations.

to Sarin at 3.0 ppb with the results shown in Table II.

TABLE II. Effect of pre-exposure of minnows to an anticholinesterase compound (Sarin) on subsequent toxic exposures

	Subsequent exposure of 50 fish each at 3 ppb			
	After 5 days recovery		After 12 days recovery	
Initial exposure at 2.5 ppb	Pre-exposed	Controls	Pre-exposed	Controls
Number dead in 24 hours of 120 exposed: 11(9.1%)	45/50 (90%)	22/50 (44%)	20/50 (40%)	21/50 (42%)

At 2.5 ppb of Sarin about 10 percent of the minnows died in a 24-hour exposure. Based on the results of the experiment as shown in Figure 5, the ChE brain activity of the minnows would have been depressed to about 50 percent of normal. After five days in nontoxic water, the brain ChE activity would have returned to about 85 percent of normal. At this time when exposed to 3 ppb of Sarin, which caused 44 percent of control fish to die in 24 hours, 90 percent of the pre-exposed fish were killed in the same exposure time. After 12 days of recovery, the brain ChE activity returned to normal levels and the response of the pre-exposed fish was the same as that of control fish when exposed to the same concentration of Sarin.

DISCUSSION

The normal ChE activity of the three species of fish brains has been determined in this study by the rate at which the esterases in the brain split acetylcholine. The ChE activity values average from 1.4 to 2.4 micromoles per hour per mg of fresh brain tissue.

Augustinsson (1948) reports on the brain ChE of six species of marine fish. On recomputing his values to the same basis used in this report, one species, *Labrus berggylta,* has a ChE value

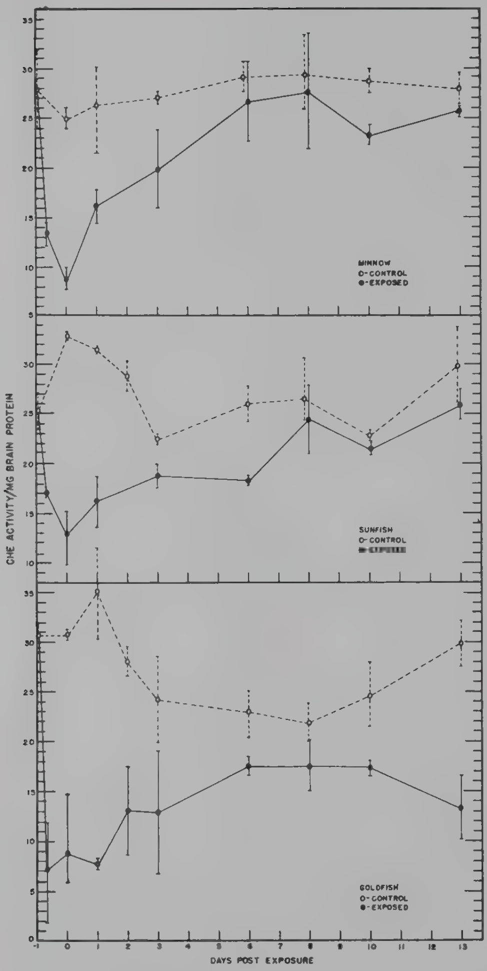

Fig. 5. The depression and recovery of brain cholinesterase in the minnow, sunfish and goldfish following exposure to cyclohexyl methylphosphonofluoridate, an anticholinesterase compound. The exposure period to the anticholinesterase material is the time from —1 to 0. The points plotted represent the average values of duplicate or triplicate samples. The limits of these values are represented by the vertical line at each point.

(1.30) of the same order of magnitude as found in the present study. The values for the other five species are lower by factors of 4 to 40. However, if all the species he reports are ranked by size (length was the only common parameter obtainable from the literature), the activity per unit brain weight appears to decrease as the average length of the species increases. This relationship holds best for those fish species having the usual length-bulk proportions and appears to follow the similar relationship between activity per unit brain weight and body weight noted for the species studied in this investigation. The change appears to be linear when fish brain weight is plotted on a logarithmic scale. This reduction in enzyme activity as the weight of brain increases has been noted in other animal forms and Nachmansohn (1939) has suggested that the change is related to the reduction of the frequency of the synapses as the mass of the other brain elements increases.

The purpose of this study has not been to consider the role of ChE in the physiological functioning of the fish but rather to investigate how the determination of brain ChE activity can be used in the assessment of the presence of anti-ChE materials in aquatic media. With the introduction of DDT, development of insecticides has taken a new turn in that these compounds are not only lethal to the harmful or undesirable insects but in the dosages used are lethal to many other associated animal forms (Springer, 1956). Compounding the danger is the development of resistance to an insecticide by the specific species under attack, which brings forth renewed applications either at higher dosages or with new classes of compounds. The organophosphorous insecticides have been demonstrated as having unusual high toxicity to flies and mosquitoes, and because of the nature of the habitat in which mosquitoes are usually found these compounds may be applied directly over or into water, particularly in larviciding operations. The use of the highly toxic insecticides in agricultural applications has led to fish kills when rains following application have washed sufficient insecticide from the land into receiving bodies of water (Young and Nicholson, 1951).

Lakes and streams which have become contaminated by anti-ChE insecticides may be assessed as to the hazard to their aquatic life by determination of the brain ChE activity of the indigenous fish. Low levels of contamination may not be lethal to the fish but continued exposure could reduce cholinesterase activity of the brain tissue and render the fish more susceptible to further exposure to the anticholinesterase materials. Normal levels of brain ChE activity would have to be determined for the same species taken from noncontaminated water.

Summary

1. The ChE activity of the brain tissue of *Pimephales promelas, Lepomis cyanellus,* and *Carassius auratus* has been determined using acetylcholine as the substrate.

2. ChE activity per unit brain weight varies

inversely but not linearly with the total brain weight.

3. Exposure of fish to anticholinesterase materials reduces the brain ChE activity with death occurring when the activity level falls to 30-60 percent of normal.

4. Recovery of ChE activity to normal levels takes approximately two weeks, following sublethal exposure.

5. Pre-exposure to anticholinesterase materials renders fish more susceptible to subsequent exposure in the recovery period.

ACKNOWLEDGMENTS

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DEMOGRAPHIC RESPONSES OF TWO HOUSE MOUSE POPULATIONS TO MODERATE SUPPRESSION MEASURES WITH 1080 RODENTICIDE[1]

John T. Emlen, Jr.,[2] Howard Young,[3] and Robert L. Strecker[4]

Introduction

Poisoning procedures used in mouse control operations often suppress an infestation without eliminating it; after an initial decline, the population apparently becomes more or less stabilized at a lower level. The mechanisms which underly this adjustment hold considerable interest for both the population ecologist and the pest control operator.

During 1948 and 1949 an attempt was made to analyze the responses of a natural infestation of house mice (*Mus musculus*) to the withdrawal of poison after a period of 33 months in which professional control operations with 1080 (sodium fluoracetate) rodenticide had consistently failed to provide more than what was considered "moderate control." This study (population *A*) was supplemented with another study (population *B*), made concurrently, in which population changes were analyzed as poisoning procedures were instituted. In both cases measurements were made of population size, mortality rates, life expectancy, population composition, breeding activity, local movements, trap susceptibility and poison susceptibility. Reports on the latter three aspects of the study have already been published (Young, Strecker and Emlen, 1950; Young, Neess and Emlen, 1952; Emlen and Crow, 1951). Data were collected over a period of eight months from September 28, 1948 to June 1, 1949. The first four months provided information on conditions before poison was removed in population *A* and before it was introduced in population *B*. The second four months provided the data for evaluation of the changes induced by poison withdrawal and poison introduction.

The studies were made in two old vivarium buildings at the University of Wisconsin in Madison. Both buildings contained much natural mouse harborage and an abundant supply of food, provided for the experimental animals such as rabbits, doves, and chickens, but constantly available to the wild mice. Both buildings were maintained at room temperatures and were dark at night. Both were reasonably isolated from other mouse infested buildings, and their populations were thus essentially unaffected by ingress and egress. Traps set in large numbers in neighboring buildings captured over 500 mice, of which only 2 were marked animals from the populations under study.

Sodium fluoracetate is a highly toxic and essentially tasteless rodenticide giving excellent results in laboratory tests (Anon., 1952). Field tests on house mice may give complete kills under optimum conditions; but populations often persist, especially where bait stations are inadequately distributed as in the present instance (Emlen, 1950). The poisoning procedure followed in this study used a one percent water solution distributed in one pint chicken drinking-wells, permanently maintained and refilled once each month. There were 18 wells or "stations" in building *A*, an average of one every 722 square feet of floor, and 8 in building *B*, an average of one every 622 square feet. Stations were distributed primarily in accordance with evidence of mouse activity, but no point in either building was more than 25 feet from a poison source.

Population data were obtained by three sampling techniques: (1) live traps were maintained in both buildings and operated three consecutive nights each week throughout the eight months of the study. A total of 1781 mice was thus captured, toe-clipped for subsequent identification, and released. By using combinations of toe-clippings on both front feet and hind feet each mouse received a distinctive marking usable for individual identification on recapture or recovery. (2) Dead mice (eventually totalling 514) found near the poison stations and elsewhere were collected and examined at each visit. (3) In each of the two buildings, the study was terminated with an intensive snap-trapping campaign carried on over a fifteen day period until capture rates had declined to near zero. A total of nearly 900 mice from this source was available for autopsy.

These sampling techniques rarely took any nestlings or young weanlings. The figures and indices to be presented are thus applicable only to the adult segment of the populations.

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RESULTS

Indices of varying reliability and value were obtained on population size, survival rates and reproductive rates.

Population size

Data on population size and the suppressive effects of poisoning operations on numbers were obtained by three methods: (1) direct tallies of animals caught in the final cleanup; (2) capture-recovery indices; and (3) records of trap success.

The total catch obtained in the snap-trapping campaigns at the end of the study provides an approach to the absolute size of the two populations at that time. The number of animals taken in 15 days of intensive trapping was 753 in population *A* and 129 in population *B*. Using the per cent capture of surviving marked mice indicated in the survival curves (Figures 1 and 2), as a measure of completeness in the snap-trapping, we may conclude that our efforts were about 80 percent successful in population *A* and about 75 percent successful in population *B*, and that the population levels were of the order of 930 (7.2 per 100 sq. feet.) in building *A* and 220 (4.4 per 100 sq. ft.) in building *B* at the end of the study.

In order to obtain data on population changes, calculations of population size at monthly intervals were essayed. The Lincoln-Peterson index based on recapture rates of marked animals (Peterson, 1896) gave erratically fluctuating and clearly unreliable figures in the present study. This presumably resulted from failure of the populations to meet certain conditions necessary for the successful employment of the equation, namely, random mixing of marked and unmarked animals, and uniform susceptibility to capture of all mice. Special analysis of our data on localization of movements (Young, Strecker & Emlen, 1950) and on heterogeneity of trap response (Young, Neess & Emlen, 1952) indicated that neither of these two basic premises were met.

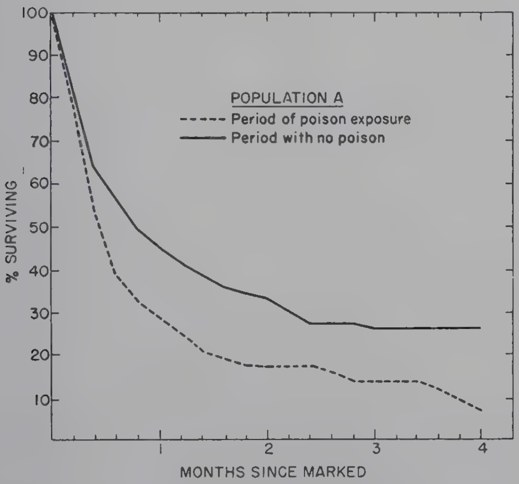

FIG. 1. Survival curve of population A during exposure to 1080 poison (dashed line) and following the removal of poison (solid line).

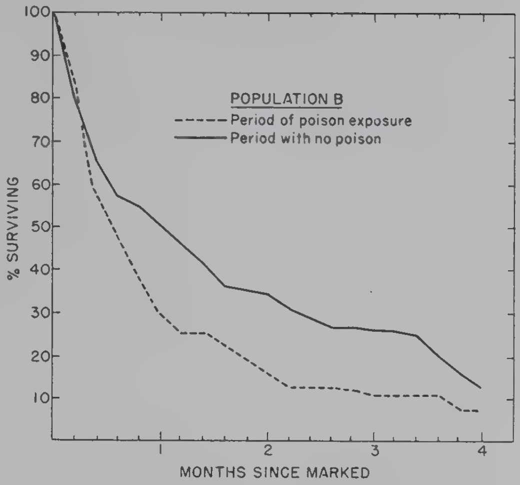

FIG. 2. Survival curve of population B before exposure to 1080 poison (solid line) and during exposure (dashed line).

Our best source of information on changes of population levels during the course of the study was trap success data (Table I). Removal of poison from building *A* was followed by an increase in trap success from 0.234 to 0.272 captures per trap night; introduction of poison into building *B* was followed by a comparable decrease in trap success. If we can assume that these indices reflect the population levels before and after poison exposure with equal fidelity, the permanent suppressive effect of treatment in both cases was of the order of 14 to 18 per cent.

MORTALITY AND SURVIVAL

Regular counts of carcasses accumulating near the poison stations indicated a prompt cessation of poison deaths after the removal of the poison wells in population *A*. In population *B* carcasses appeared in large numbers immediately following the introduction of poison, continued at a high level through February and March (118 and 112) and then declined in April and May (38 and 37) (Table V). A reduction in the number of observed carcasses after the first few days or weeks is characteristic of poison campaigns and is generally thought to reflect and parallel the popula-

TABLE I. Trap success data (captures per trap night) during and after poison exposure in population *A*; before and during poison exposure in population *B**. (Data for poisoned populations are italicized; figures in parentheses represent 95 per cent confidence range)

Month	Population A		Population B	
	Catch	Trap Success	Catch	Trap Success
	(poison present)		(before poison introduced)	
Oct.....	*245*	*.23*	129	.25
Nov....	*184*	*.22*	94	.22
Dec.....	*153*	*.25*	93	.23
Jan.....	*199*	*.24*	96	.23
4 mos... average	...	*.234* (.220 – .248)	...	.234 (.214 – .254)
	(after poison removed)		(poison present)	
Feb.....	209	.25	*80*	*.19*
Mar.....	277	.28	*104*	*.21*
Apr.....	257	.33	*88*	*.21*
May....	190	.23	*68*	*.16*
4 mos... average	...	.272 (.256 – .288)	...	*.193* *(.175 – .211)*

*Trap success figures are not comparable between colony A and colony B because of different population-trap density ratios.

tion reduction. Since a general and marked reduction in population level did not occur in late March in our study the decline in carcass accumulation must be explained otherwise, probably by assuming local reductions among sedentary population segments near the poison stations.

Mortality rates are usually difficult or impossible to measure in free-living populations. Mortality data, however, are available for the marked segment of our study populations. The number of deaths of marked mice each month was determined simply by relating the gain (+) or loss (—) of marked mice in the population to the number introduced (marked and released) during that month. The montly mortality rate for marked mice derived from these figures should, we feel, be representative of the rate for the whole population.

Table II presents these data. The second column designated increment (*I*) gives the actual figures of mice trapped, marked and released into the population each month. The fourth column (*N*) shows the number of marked mice present at the end of the month as determined from records of individual survival based on subsequently recovery. These, of course, are minimum figures rather than approximations of the actual number, but they approach the actual number quite closely and would appear to be entirely suitable for deriving indices for comparing pre- and post-treatment conditions. The third column (*M*) gives the number of deaths during the month, determined by subtracting the net gain in numbers over the previous month ($N_p - N_{p-1}$) from the increment (*I*). The mortality rate figure (*M/N*) is derived by dividing the mortality (*M*) by the number of mice present (the mean of the number present at the end of the month and that present at the end of the preceding month) and multiplying by 100.

TABLE II. Data on monthly increments (*I*) and population levels (*N*) of marked mice before, during and after poisonings together with computed values of monthly mortality (*M*) and mortality rates (*M/N*). (Data for poisoned populations are italicized.) (Further explanation in text)

Month	Population A				Population B			
	I	M	N	M/N	I	M	N	M/N
	(poison present)				(before poison)			
Oct.......	*192*	*125*	*67*	...	104	67	37	...
Nov.......	*140*	*129*	*78*	*178*	57	44	50	100
Dec.......	*95*	*103*	*70*	*139*	63	47	66	81
Jan.......	*139*	*119*	*90*	*149*	53	44	75	62
	(after poison)				(poison present)			
Feb.......	174	91	83	...	*73*	*37*	*36*	...
Mar.......	205	158	130	147	*75*	*76*	*35*	*211*
Apr.......	175	134	171	89	*65*	*54*	*46*	*132*
May.......	139	130	180	74	*42*	*44*	*44*	*98*

The records for population *A* in November may be used to illustrate these calculation procedures. The five 3-day trapping operations during this month captured 140 animals which were marked by toe clipping and promptly returned at the site of capture. The number of animals in the marked segment of the population was thus augmented by 140 (*I*) during the month. Trapping activities over the succeeding six months, including the terminal snap-trapping campaign, gave positive evidence of 67 marked animals present as of October 31, and 78 as of November 30. There was thus an apparent gain of 11 animals in the marked segment during the period in which 140 were added, so the indicated mortality (*M*) was 129 animals. This number divided by the mean number present during the month ($67 + 78/2$) provides a figure ($M/N = 178$) which, though not a conventional measure of mortality rate, appears to be the best indicator for analysing mortality trends during the course of this study.

This index of mortality rate in population *B* varied between 62 and 100 (avg. 81) per month before poisoning, rose to over 200 per month when control operations were introduced, then gradually declined to about 100. In population *A*, the indicated mortality rate was between 139 and 177 (avg. 155) per month while poison was present. It remained high for two months after removing the wells, then dropped to below 100. Since variables are numerous and sample sizes small, these figures should not be interpreted as absolute measures of mortality rate. They would, however, appear to have value as indicators of change and, as such, they suggest a 2- to 3-fold jump in mortality rate following initial exposure, and a trend toward return to the pre-poison level during continued exposure.

Another parameter available for comparing poison and no-poison periods is mean life-expectancy for each animal from the time of first capture. Complete data are lacking, but a satisfactory index was devised based on days survived divided by days available (remaining until termination of the study). Records of 677 recovered marked mice were used in these analyses. Figure 1 compares the survival of population *A* mice during poisoned and unpoisoned periods and Figure 2 does the same for population *B*. These curves were derived by computing the days survived by each mouse after it had been marked, using the last record of any given individual as its mortality date. Computations were made in two ways; in the first only animals that were recaptured were used, in the other, all marked animals were considered, those never recovered being recorded as having survived zero days. The first system obviously over-estimates survival, since the reason some mice do not re-enter traps is that they have died. The second under-estimates survival, since some mice still in the population will not re-enter traps (Young, Neess & Emlen, 1952). The values used in preparing the survival curves in Figures 1 and 2 are the averages of the figures obtained by these two methods. They are obviously only estimates at best, but since the error sources are presumably the same in each time period, they should be valid for purposes of comparing pre- and post-treatment conditions. The marked animals on which these computations are based constituted roughly one fourth of the total population in each case (21.9 percent in *A* and 28.7 percent in *B* at the final snap-trapping).

Examination of Figure 1 shows that in population *A* survival was considerably greater after removal of the 1080 wells than before: 26 percent as against about 10 percent at the end of four months. The poisoning operation had thus had a pronounced depressing effect on survival, though this was insufficient to give population control. Figure 2 shows a similar depressing effect of poison operations on survival in population *B*. The response to poison in this initial exposure in *B* was apparently no different from that in population *A* where the poison had been used continuously for nearly three years.

Since these mice were trapped and marked at varying times, their survival extended over different periods, during which various changes in environment and demography could have occurred. The effects of this variability are masked in Figures 1 and 2. A more stable indicator of survival for comparing poison and non-poison periods is obtained when the rate is given for bi-monthly intervals (Table III). Averaged in this fashion these data show a definite but moderate effect of poison operations on survival.

TABLE III. Life expectancy indices (days survived/days available) before, during and after poison exposure. (Data for the poison periods are italicized)

Population	Oct.-Nov.	Dec.-Jan.	Feb.-Mar.	Apr.-May
A...........	*.340*	*.325*	.398	.464
B...........	.404	.441	*.329*	*.363*

The indices of life expectancy used in these curves and averages are, of course, not measures of actual survival. The technique utilizes animals of undetermined and varying ages, and it omits the unknown period between last capture and actual death in those not finally recovered. These indeterminate variables make it impossible for us to express our data in absolute units such as days. The figures are quite satisfactory, however, for accomplishing our objective of comparing survival before and after poison exposure.

Reproductive Rates

Data on reproductive activity were obtained from analyses of sex ratios, age composition and the reproductive condition of animals in trapped samples (Tables IV and V). Sex ratios showed no consistent changes associated with poison operations. In the age composition data, the rise from 34 to 42 non-breeding immatures per 100 adults with the introduction of poison in population *B* and the drop from 23 to 19 with the removal of poison in population *A* are suggestive of a population adjustment, but month to month fluctuations were great and the figures have no statistical significance. Data on sexual activity as read by the incidence of scrotal testes among males and of perforated vaginal orifice among females also fluctuated markedly from month to month and revealed no consistent change with the introduction or withdrawal of poison. Reliable

TABLE IV. Sex and age composition of mice in colony *A*. (Data for the poison period are italicized)

Month	Immature* ♂	Immature* ♀	Adults ♂	Adults ♀	Immatures per 100 adults	% ♂♂ among adults
a. Live Trap Samples						
Oct. 1948	*24*	*18*	*109*	*93*	*21*	*54*
Nov. 1948	*9*	*14*	*85*	*74*	*14*	*53*
Dec. 1948	*17*	*21*	*62*	*53*	*33*	*54*
Jan. 1949	*17*	*24*	*93*	*63*	*26*	*59*
Poison period totals	*67*	*77*	*349*	*283*	*23*	*55*
Feb. 1949	9	23	98	81	18	54
Mar. 1949	25	32	120	100	26	55
Apr. 1949	18	26	120	93	21	56
May 1949	11	9	88	82	12	52
Post-poison totals	63	90	426	356	19	54
b. Poison killed samples (found dead)						
Oct. 1948	*7*	*2*	*20*	*10*	*30*	*67*
Nov. 1948	*2*	*11*	*19*	*20*	*32*	*49*
Dec. 1948	*3*	*10*	*37*	*21*	*21*	*64*
Jan. 1949	*8*	*16*	*8*	*15*	*104*	*29*
Totals	*20*	*39*	*84*	*66*	*39*	*56*
c. Snap trap samples						
May 1949	76	134	263	270	39	49

*Under 15 grams.

TABLE V. Sex and age composition of mice in colony *B*. Data for the poison period are italicized

Month	Immature* ♂	Immature* ♀	Adults ♂	Adults ♀	Immatures per 100 adults	% ♂♂ among adults
a. Live Trap Samples						
Oct. 1948	22	19	60	32	45	65
Nov. 1948	12	6	39	37	24	51
Dec. 1948	12	11	37	33	33	53
Jan. 1949	11	13	32	39	34	45
Pre-poison totals	57	49	168	141	34	54
Feb. 1949	*15*	*8*	*30*	*27*	*40*	*53*
Mar. 1949	*14*	*13*	*39*	*38*	*35*	*51*
Apr. 1949	*12*	*15*	*31*	*30*	*44*	*51*
May 1949	*5*	*19*	*18*	*.6*	*55*	*41*
Poison period totals	*46*	*55*	*118*	*121*	*42*	*49*
b. Poison killed samples (found dead)						
Feb. 1949	*17*	*23*	*43*	*35*	*51*	*56*
Mar. 1949	*10*	*25*	*42*	*35*	*45*	*55*
Apr. 1949	*4*	*10*	*16*	*8*	*58*	*67*
May 1949	*4*	*7*	*14*	*12*	*42*	*54*
Totals	*35*	*65*	*115*	*90*	*49*	*56*
c. Snap trap samples						
May 1949	*14*	*31*	*37*	*43*	*56*	*46*

*Under 15 grams.

data on prevalence of pregnancy and litter size were obtained only from dead animals collected in the final snap trapping or picked up incidentally during live-trapping operations. The samples are thus inadequate for meaningful comparison of pre- and post-poison periods and may be biased by a selective effect of trapping as compared with deaths from poison. The insignificant rise of pregnancy in population *A* from 36 percent (59 adult females autopsied) during the poison period to 39 percent (207) in the final snap trapping four months after poison removal suggests an absence of any major adjustment in breeding activity. Carcass samples from population *B* (15 adult females) were too small to hold any suggestive value, and the snap trap sample of 48 animals revealing a 47 percent pregnancy incidence is difficult to evaluate. It is thus impossible to draw any conclusions as to the occurrence or nature of any reproductive response which these populations may have made to the introduction or removal of poison.

DISCUSSION

Data obtained in this study are not adequate to permit the construction of precise population models showing before and after balances of population parameters. The independent measurements of population level, mortality rate and life expectancy do, however, show general agreement (Figure 3) and permit the formulation of certain conclusions concerning the regulating mechanisms of these free-living populations and their responses to poison exposure of the type here employed.

The effects of poison removal in population *A* were essentially the reciprocal of the effects of poison introduction in population *B*. This seems to indicate that the release from long-sustained poison exposure resulted in adjustments essentially opposite to and balancing those imposed by first exposure. There was no evidence that the continuous exposure of population *A* for 33 months had any effect on poison susceptibility or on the basic mechanisms of population regulation (Emlen and Crow, 1951).

The response to the introduction of a poison as observed in population *B* may be divided into two phases: (1) an initial reduction phase in which the population was reduced by about 18 percent, and (2) a second phase in which the population became more or less stabilized at the new depressed level. The reduction phase was characterized by a high mortality rate (Figure 3B-b) and a sharply reduced life expectancy (Figure 3B-c). The large accumulation of poisoned carcasses (Figure 3B-d) suggests that the poison was responsible for these disturbances and probably accounted for a majority of the deaths which effected the population reduction.

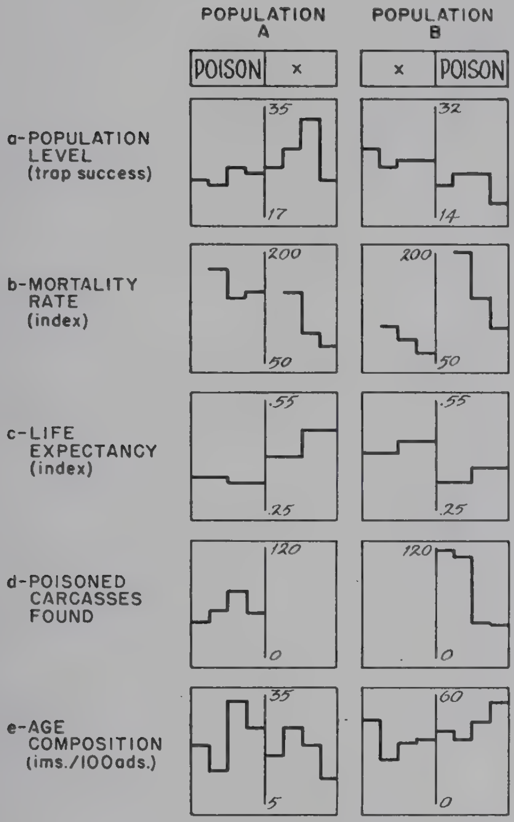

Fig. 3. Before and after poison trends in various population parameters. The scale of the vertical axis in each case is in arithmetic intervals but in floating except in d. Actual measurements are contained in Tables I to V.

Special significance must be attached to the failure of these trends to continue, and the apparent restabilization of the population at a new depressed level comparable to that found in population *A* after a long period of poison exposure. This stabilization could be accounted for by (1) a compensatory adjustment of recruitment to meet the increased mortality or (2) a cessation of the supplementary mortality caused by the poison. We have no clear evidence that the former mechanism operated in this case, though a slight increase in the proportion of young mice in the population (Figure 3B-c) suggests that it might have contributed. Clear evidence for a substantial decrease in the poison mortality is provided, however, by the trends in mortality rate, life expectancy, and carcass accumulation. It seems quite certain that this must have been the principal mechanism involved.

We have seen that the indicated reduction in poison deaths cannot be attributed to acquired immunity or to selection. It is readily explained, however, if the effectiveness of the poison was spatially limited to the vicinity of the stations and failed to reach substantially into the intervening areas. Under such conditions severe decimation of the localized population units living near the stations would result in a moderate overall decline of the type observed during reduction, and the attainment of virtual extirpation in these units would produce the indicated check in the downward trend of the population as a whole. We have no direct evidence that this localized extirpation occurred, but our demonstration that mice in these colonies had an average cruising radius of only about 6 feet (Young, Strecker and Emlen, 1950) suggests that only a small fraction of the total population was intimately exposed to the poison sources which were spaced at an average of about 30 feet. It may well be that the great majority of poison deaths occurred in these local segments and that the relatively slight response of the population as a whole reflects the numerical dominance of the population matrix occupying the spaces between the bait stations and largely beyond their influence.

Similar conclusions were drawn by Robinson (1953) in studies of differential mortality of various predators on 1080-poisoned ranges in the western United States. Campaigns in which the poison stations were widely spaced were effective against coyotes with far-ranging habits but only of small and local value in reducing the more sedentary skunks, kit foxes, and badgers. These results were interpreted as indicating that the number of bait stations or traps used in population control should be related to the home range characteristics of the species in question.

The behavior of population *A* upon removal of the poison is more difficult to interpret. The population recovery apparently started slowly and extended over three months, then unaccountably dropped (Figure 3A-a). Mortality rates declined after a two-month delay (Figure 3A-b), and life expectancy showed a continuing increase to the termination of the study (Figure 3A-c).

This delayed response of the various population parameters may reflect a gradual dispersal of the animals into depopulated areas around the poison stations. Such a movement would presumably afford temporary release from population pressures which would be reflected in changes of the type shown by our mortailty and life expectancy figures. The effects would be expected to be of brief duration, however, and we have no satisfactory explanation at this time for the continuing trends suggested by our data.

In many respects our measurements of the responses of these populations to introduction and removal of poison are crude. It is disappointing that the very considerable effort expended did not provide sufficient data for the construction of population models. The experience is by no means new, however, and we feel that our failure itself is illuminating in reemphasizing the complexity of population regulation and population responses. The extremely toxic nature of 1080 makes it particularly clear cut in its effects (nearly complete kill on a broad or, as in this case, on a local, spot pattern), but even here the complications are overwhelming. We thus conclude that populations of house mice in buildings resemble populations of many wild species in nature in being regulated by a sensitive balance between many interdependent factors of mortality and reproduction. In such a situation it is unrealistic to consider poison kill as a simple supplement to natural mortality factors. Intercompensatory effects such as those described by Errington (1946) undoubtedly exist, and an understanding of any single situation must involve a much more complete analysis than we were able to make.

SUMMARY

Two natural populations of house mice in buildings were subjected to subadequate control measures with sodium fluoracetate (1080) rodenticide. Data on population size, mortality rate, life expectancy, population composition, breeding activity, local movements and poison susceptibility were obtained over an eight month study period by live trapping, marking and releasing 1781 mice, by examining 514 dead mice as found and by autopsying 898 mice killed with snap traps at the termination of the study. In one population (*A*), poison was exposed during the first 4 months and withdrawn for the second; in the other population (*B*), it was withheld for the first period and introduced for the second.

Corrected tallies of mice captured in the terminal trapping revealed population sizes of about 930 for population *A* and 220 for *B* at this time. Application of a modified Peterson index gave meaningless figures of population changes during the study period, but trap success data suggested an increase of about 14 percent in population *A* after poison removal and a decrease of about 18 percent in population *B* after poison introduction.

Monthly mortality rates determined for the marked segment of the population and considered representative of the total population dropped to about one half with the removal of poison in population *A*. Concurrently they nearly doubled with the introduction of poison in population *B*. A life-expectancy index showed a rise of about 30 percent with poison removal in population *A* and a drop of about 20 percent with poison introduction in population *B*.

The population response to poison introduction was essentially the reciprocal of that to poison removal. Mortality and life expectancy were disturbed while the population was declining following poison introduction and then tended to recover as the population stabilized. Following poison removal, mortality and life expectancy were again disturbed during the period of population readjustment, but the indicated trends were confusing and the relationships obscure. Most of the data suggest that the observed overall reduction under poison exposure was effected and maintained by a heavy reduction in the areas closely surrounding the poison stations, and that the animals inhabiting the broad intervening spaces were largely unaffected.

The failure to obtain data suitable for a clear analysis of population responses is attributed to the complexity of interactions of many factors of mortality and regulation and to intercompensating mechanisms which mask and confuse the effect of a single artificially introduced mortality factor.

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FACTORS INFLUENCING THE DISTRIBUTION OF BEES' NESTS IN EARTH BANKS

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Introduction

It has long been observed that many species of solitary and primitively social burrowing bees make nests in large groups. Sometimes these aggregations of apparently independent nests are compact and well delimited, in other cases they are diffuse, and finally, many species construct nests so scattered that it seems purely chance if two are close together. Some students of the behavior of bees have believed that groups of nests occur as a result of a tendency of certain species of bees to aggregate (perhaps taking the form of a tendency for progeny to return to the vicinity of their parental nest to make new nests). Others believe that groups arise, not as a result of any innate aggregation factor in the bees, but because of habitat requirements or preferences. According to this idea, the bees which nest in groups do so simply because the environment is optimum for nesting in localized areas, while bees whose nests are scattered either have broad habitat tolerances or occupy widely distributed habitats. No one can doubt the importance of edaphic and other environmental factors in determining where bees nest. The question remains, is there also aggregative behavior among some bees which further limits the nesting areas of these species? The present study was undertaken in order to shed light on this question. It is also intended to provide an ecological background for a series of papers on the behavior of various species of bees.

The study was made near Curitiba, Paraná, Brazil, making use of nests in a series of roadside banks, during the year July 1, 1955, to June 30, 1956.

Regional climatic data are found in works of Maack (1948), Setzer (1946) and the Instituto Quimica Agricola (1944). The climatic type is Cfb (Koeppen), BB'r (Thornthwaite) and tiUV° (Serebrenick). Maack gives the following details for Curitiba (based on the period 1885-1944):

Average annual temperature, 16.3°C; average January temperature, 20.2°C; absolute maximum temperature, 34.6°C; average July temperature, 12.0°C; absolute minimum temperature, —6.3°C; average annual precipitation, 1401 mm; average summer season (October to March) precipitation, 845 mm; average winter season (April to September) precipitation, 556 mm; year of maximum precipitation (1909), 1909 mm; year of minimum precipitation (1916), 1030 mm; average number of days of rain, 171; average number of clear days, 20.

As can be judged from the above, weather is mild in summer, cool in winter, there being periods of freezing weather practically every winter. The cool weather (for the latitude, 25° 25′ S) results from the altitude, our area of study being 910 to 947 meters above sea level, on the first plateau of Paraná, which is a part of the extensive South Brazilian Plateau system. As the rain is abundant and well distributed, the banks are always moist except sometimes for the outermost two or three centimeters.

The area studied was primitively forested, and patches of forest still exist close to the banks which we studied. The forest is dominated by the "pinheiro," *Araucaria angustifolia* (Bertol.) D. Ktze., but contains a large number of other, generally smaller, trees such as "mate" (*Ilex paraguayensis* St. Hil.), "pinheiro brabo" (*Podocarpus lambertii* K.), and especially at the margins, "aroeira" (*Schinus terebinthifolius* Raddi). Where the forest is cut, many bushes and coarse herbs grow, some of which (*e.g., Baccharis* spp., *Eupatorium* spp., *Senecio brasiliensis* Less., *Solanum* spp., and *Hyptis sinuata* Pohl) have flowers which are attractive to bees. As shown by Maack (1950), however, Curitiba is at the margin of a grassland area, and natural grasslands exist within a few kilometers of the area studied.

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In spite of low temperatures, the fauna has a predominantly tropical aspect. For example, various species of *Morpho, Caligo, Heliconius,* and other tropical groups of butterflies are not only present but very common in summer; and some 20 species of stingless honey bees (Meliponini) occur in the environs of Curitiba. (Only one reaches as far south as Buenos Aires, over 40 have been found in the vicinity of Belém, at the mouth of the Amazon, and 42 in Panama.) On the other hand, many strictly tropical types do not reach Curitiba, doubtless because of the cold.

BEES STUDIED

The bees found nesting in the banks are as follows:

Family Colletidae

1. *Perditomorpha brunerii* Ashmead, 1899
2. *Bicolletes iheringi* (Schrottky, 1910)
3. *Lonchopria cingulata* Moure, 1956
4. *Belopria zonata* Moure, 1956
5. *Colletes kerri* Moure, 1956
6. *Colletes michenerianus* Moure, 1956
7. *Colletes rugicollis* Friese, 1900

Family Andrenidae

8. *Pseudopanurgus* sp?

Family Halictidae

9. *Augochloropsis diversipennis* (Lepeletier, 1841)
10. *Augochloropsis sparsilis* (Vachal, 1903)
11. *Caenaugochlora curticeps* (Vachal, 1903)
12. *Pseudaugochlora nigromarginata* (Spinola, 1841)
13. *Habralictus canaliculatus* Moure, 1941
14. *Augochlorella michaelis* (Vachal, 1911)
15. *Neocorynura polybioides* (Ducke, 1906)
16. *Paroxystoglossa andromache* (Schrottky, 1909)
17. *Pseudagapostemon cyanomelas* Moure, 1957
18. *Pseudagapostemon divaricatus* (Vachal, 1903)
19. *Chloralictus*[5] *rhytidophorus* Moure, 1956
20. *Chloralictus seabrai* Moure, 1956
21. *Chloralictus* spp.

Family Megachilidae

22. *Megachile* spp.

Family Apidae

23. *Paratetrapedia oligotricha* (Moure, 1941)
24. *Monoeca* sp?
25. *Melitoma euglossoides* Lepeletier and Serville, 1828
26. *Anthophora paranensis* Holmberg, 1903
27. *Thygater analis* (Lepeletier, 1841)

In subsequent parts of this paper, reference to a bee by genus only indicates the species listed above.

It is an interesting fact that many of these bees were rare or even absent in the collection of Padre J. S. Moure, made by collecting from flowers over a period of years in the vicinity of Curitiba. We assume that this means that the commoner bees in the area (and probably any area) are those that nest in flat ground. Although the bees nesting in banks may be common enough in the banks, the small nesting space available limits in the populations and makes them generally less common on flowers than bees nesting in flat ground. Incidentally, bank inhabitants are probably much more common now because of roadside banks than under primitive conditions when they had to rely on natural erosion to provide nesting sites.

THE BANKS

The series of roadside banks studied are west of the city of Curitiba, 2.5 km west of the meteorological station in the bairro of Mêrces, in the rolling land close to the right hand side of the Rio Bariquí. The extent of the banks can easily be seen from Figure 1. This figure shows also our division of the 1722 meters of banks into 492 divisions, each 3.5 meters long. In height the banks range from less than a meter to four meters. The direction of the banks can be seen from Figure 1, from which an idea of variations in insolation can be obtained. All are approximately vertical (see Fig. 3), except that in divisions 117 to 119 there is a strong overhang so that the banks below are permanently shaded. The age of the banks at the end of the study period was as follows: Divisions 1 to 320 and 401 to 460, 70 years or more (naturally, as the road has been widened and the cuts deepened, the banks have changed some but the change in any one year has probably been very small); divisions 321 to 400, about 5 years; divisions 461 to 492, about 14 months. The majority of the nests were in the older banks but this could not be attributed to the age of the banks with any certainty.

The soil and subsoil of the banks are varied, as described below. An account of soils of the area in general was given by Cavallar-Kavaleridze (1955). The underlying rock is nearly all gneiss

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[5] We are tentatively following Padre J. S. Moure in recognizing *Chloralictus* as genus, although this is contrary to established practice elsewhere in the world and further study may show it to be incorrect.

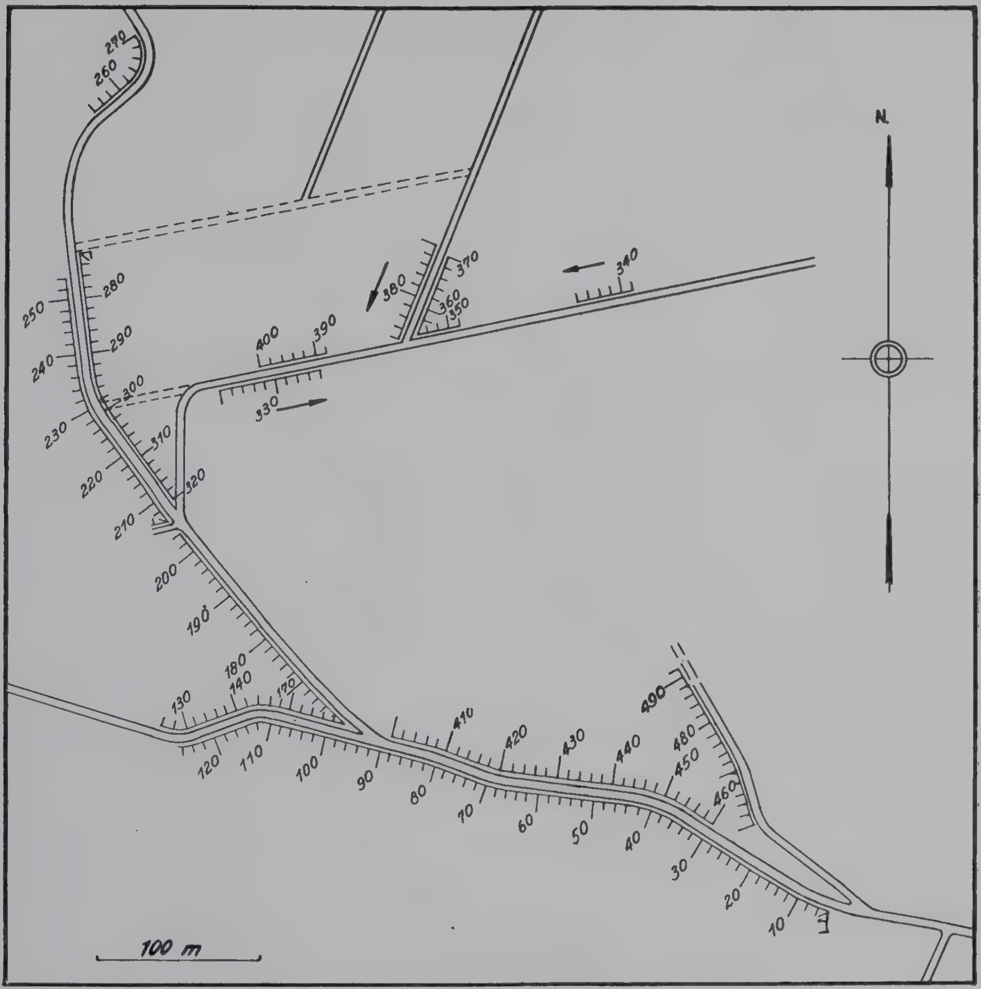

FIG. 1. Map of roadside banks described in this paper, divided into numbered divisions, each of which is 3.5 meters long.

which is considered as Archean in age by some authors (*e.g.* Oliveira, 1927, and Carvalho, 1936), and as the Proterozoic Açunguí series, remetamorphosed, by others (*e.g.* Maack, 1947). These rocks grade into typical Açunguí some 15 miles northwest of Curitiba. The gneiss contains intrusions of diabase in the form of dikes. A very small dike occurs in the midst of our area of study but no bee nests were found in the decomposed diabase there; divisions 339 to 348 are also in soil formed from a decomposing dike of diabase. These divisions contain nests of one species of bee (*Pseudaugochlora*) which also nests in the decomposed gneiss. Unfortunately there was not enough diabase in the area to make possible a significant comparison between decomposed gneiss and decomposed diabase as nesting soils and subsequent sections of this paper deal with soils produced from the gneiss.

Weathering has resulted in a decomposition of the bedrock to a depth of two to ten meters. The majority of the banks do not reach the bedrock, but in a few places it is visible. Above the bedrock, the decomposition of the various components of the gneiss is clearly evident. The feldspars are completely altered into clay minerals, predominantly kaolinite, and soluble leached products. The iron-magnesium minerals furnish, as products of chemical alteration, relatively high percentages of clay minerals and soluble products, but also, with oxidation, iron hydrates that form the pigment of the mantle. The quartz apparently

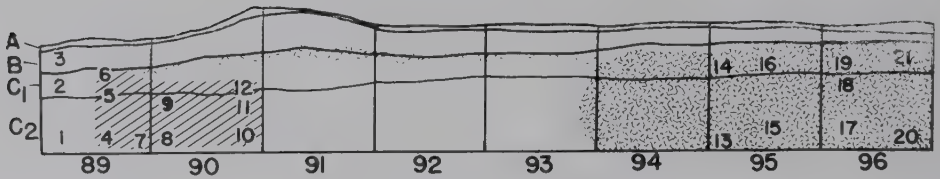

FIG. 2. Diagram of a section of roadside bank containing divisions 89 to 96, each of which is 3.5 meters long. Soil layers or horizons are indicated at the left, division numbers across the bottom. Other numbers indicate locations for soil samples listed in Table II. The area shaded by parallel lines is occupied by nests of *Augochloropsis sparsilis;* the other shaded area, by *Lonchopria,* with lighter shading indicating a region of sparse nests of this bee. Locations of nests of other species, less common in these divisions, are omitted. Details of numbers of nests per division are indicated in Table I.

suffered no decomposition and remains as sand, pebbles, or cobbles in otherwise decomposed material.

From top to bottom of the soil and decomposed rock there is, naturally, progressively less alteration. In a typical profile, such as can be seen in the banks studied, one can note the following sequence of layers or horizons:

A_1: Dark brown, granular surface layer. Ratio $SiO_2/Al_2O_3 = 2.4$. Percentage of humus, 3.2.

A_2: Brown eluvial layer with coarse granular structure. Percentage of humus, 1.4.

B: Reddish brown illuvial layer with coarse prismatic structure, rich in colloids. Ratio $SiO_2/Al_2O_3 = 1.9$, indicating incipient lateritization. At the lower margin of this layer there is usually a thin band, often double or irregular, of angular quartz pebbles, indicating the Pleistocene surface or surfaces which developed under arid climatic conditions. (For information on past climates, see Maack, 1948.)

C_1: Decomposed gneiss which has lost the gneissic structure and sometimes, due to soil creep, is no longer in the primitive position. Ratio $SiO_2/Al_2O_3 = 2.4$.

C_2: Decomopsed gneiss which is soft but yet retains the gneissic structure and rests on solid gneiss.

FIG. 3. One of the banks, starting at division 90 and disappearing in the distance at about division 110. The large trees are *Araucaria angustifolia.*

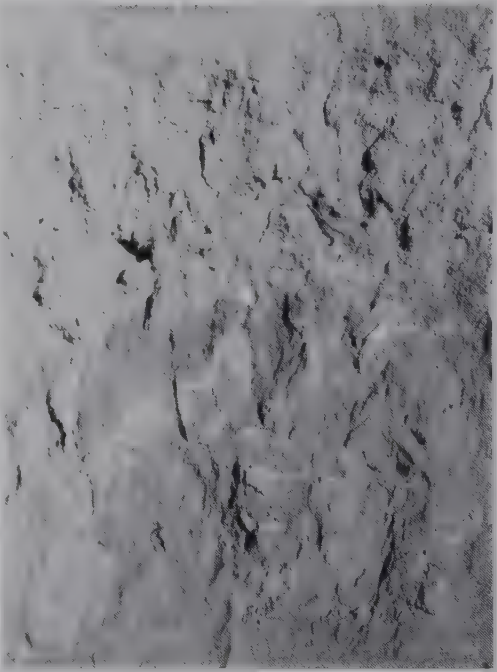

FIG. 4. A portion of a bank showing the difference between the two important soil layers on a surface which had not been disturbed by man for at least a year. Soil layer B is above, showing numerous cracks and appearing dry; layer C_1 (grading into C_2 at bottom of picture) is below, and shows few cracks (none in C_2) and moist appearance. Between B and C can be seen white quartz pebbles, in this case irregularly placed, marking Pleistocene soil surface developed under dry conditions.

The contrasting appearance of horizons B and C_1 on a bank which was well weathered and not recently disturbed is shown in Figure 4.

Of course these horizons are not identical in all divisions. Thus in divisions 426 to 492 layers A, B, and C_1 have been scraped off mechanically.

In a few areas, notably divisions 117 to 126 and 255 to 270, layer C_1 is absent and there is a thin sheet of hardpan at the bottom of B. In the majority of divisions, however, C_1 ranges from several centimeters to over a meter in thickness. In some areas where soil creep has occurred, it contains masses of decomposed gneiss (C_2) above the level of the main mass of the latter. The illuvial and eluvial soils (A_2 and B) also vary from nearly absent, in a few places, to a depth of two meters or more. Of course not all portions of the roads are equally deeply cut; the shallower cuts expose only the more superficial layers of soil. Therefore many of the divisions marked in Figure 1 lack or nearly lack exposures of layers C_1 and C_2.

On the bank surfaces, the eluvial and illuvial layers (A_2 and B) are hard, usually full of cracks, and look very dry even when the soil within is reasonably moist. Pieces of soil readily fall off in most places. By contrast the layers of decomposed gneiss (C_1 and especially C_2) are relatively soft, usually entirely without cracks, and except in dryest weather, look a little moist.

Distribution of Nests

The great majority of the bee nests studied were in layer C_2 although many also occurred in C_1. Perhaps the number of nests found in the latter is less only because its exposed area is less (see Table I). We have the impression, however, that there are usually more nests in the lower part of layer C_1 where it is grading into C_2. The division between these two layers is usually arbitrary. Above layer C_1 the only burrowing bees found were *Melitoma* and perhaps a few nests of *Lonchopria*. Nests of a few species of *Megachile* were also found in cracks or in holes left by decomposed roots in the illuvial and eluvial soils, but these bees use whatever small cavities they can find, probably with little regard for location (Michener 1953).

Of the species of bees listed above, several (numbers 1, 7, 8, 14, 21, 22, and 24) were so rare in these banks that they add nothing to our knowledge of distribution of bee's nests. Others were also scarce, but their distribution in the banks was possibly meaningful. These are as follows:

Bicolletes iheringi. Eight nests, in division 119, in shade under overhang, all in area about 10 cm in diameter.

Colletes kerri. One nest each in the following divisions: 9, 73, 413, and 415; two nests in 417.

Colletes michenerianus. Five nests, all in division 320.

Caenaugochlora curticeps. Five nests found, one in division 89, three in 111, and one in 153.

Habralictus canaliculatus. Four nests found, two in division 90, one each in divisions 107 and 185.

Pseudaugochlora nigromarginata. Eleven nests found, located as follows: 96, 98(2), 106, 161, 344 (3), 340 (2), 467.

Neocorynura polybioides. Eleven nests in shade under overhang, divisions 117 (10) and 118 (1).

Paroxystoglossa andromache. Six nests, distributed as follows: 259, 260, 261 (2), 262, 481.

Chloralictus seabrai. Six nests, distributed as follows: 89, 90 (3), 109, 450.

Anthophora paranensis. Four nests, one each in the following divisions: 96, 261, 353, 480.

Melitoma euglossoides. Sixteen nests in two areas of hard illuvial soil in the following divisions: 11 (10), 50, 51 (5).

The remaining bees were sufficiently common that the distribution of their nests should indicate something as to aggregative tendencies. They are listed in Table I, together with nest locations. Only soil layers C_1 and C_2 are considered in calculating the areas available to bees, and *Melitoma* nests (layer B) are entirely excluded from the totals in that table. To reduce the size of the table, no divisions with less than four square meters of these suitable soils were included. Few nests of the species listed in the table occurred in divisions with less than this area of such soils. However, the following nests of *Chloralictus rhytidophorus* were in divisions with less than four square meters of layers C_1 and C_2: division 10, 9 nests, 1.1.m^2C_2, 1.1 m^2C_1; division 272, 10 nests, 0.8m^2C_2, no C_1.

In order to shed more light on the distribution of the nests, eight divisions (89 to 96) having abundant bee nests were selected for further study. A diagram of these divisions is shown in Figure 2, with the location of the various areas of nests. Numbers indicate various soil sampling points. Results of studies of the soil samples from these locations, and from some divisions across the road facing in the opposite direction, are shown in Table II. In this table, the letters under "soil horizon" refer to the various layers of soil listed above. Particle size was determined for pebbles and sand by sieve analysis, for silt and clay by peptization with sodium oxalate followed by pipette analysis. The four particle-size classes are as follows: pebbles, between 2 mm and 64 mm in diameter (largest in our studies 4 mm); sand,

TABLE I. Bees' nests found in divisions of banks containing over four square meters of suitable soil (decomposed gneiss or diabase, layers C_1 and C_2). (The column headed "total nests" includes all species, not merely those listed in this table.)

Divisions	*Lonchopria*	*Belopria*	*A. diversipennis*	*A. sparsilis*	*P. cyanomelas*	*P. divaricatus*	*C. rhytidophorus*	*Paratetrapedia*	*Thygater*	Total nests	m² layer C_2	m² layer C_1	Exposure	Total nests/m²
1							1			1	4.2	.6	E	.2
2										0	4.1	.7	E	0
3										1	3.5	.9	NNE	.2
4										0	3.5	1.1	NNE	0
27										0	3.5	1.4	NNE	0
28										0	3.3	1.4	NNE	0
52										0	.4	3.9	N	0
54										0	2.8	2.1	N	0
55										0	5.3	1.8	N	0
56										0	6.0	1.1	N	0
57										0	6.0	1.8	N	0
58										0	6.0	1.4	N	0
59										0	4.8	1.8	N	0
60										0	4.3	.7	N	0
61										0	2.1	2.8	N	0
62										0	3.5	1.8	N	0
63										0	1.4	3.5	N	0
64										0	.4	4.2	N	0
65										0	4.8	1.1	N	0
66										0	5.3	1.8	N	0
67										0	4.2	2.8	N	0
68										0	6.7	.7	NNE	0
69										0	7.0	1.1	NNE	0
70								4	1	5	8.8	1.1	NNE	.5
71								14	1	15	8.8	1.8	NNE	1.4
72						25		5		30	9.1	1.4	NNE	2.9
73						10				10	9.8	1.1	NNE	.9
74			1			20				21	9.1	1.4	NNE	2.0
75						30				30	6.0	3.5	NNE	3.2
76			1			30				31	8.8	1.8	NNE	3.0
77			1							1	7.7	2.8	NNE	.1
78			1							1	8.4	2.8	NNE	.1
79										0	8.8	1.4	NNE	0
80										0	7.0	1.8	NNE	0
81			1							1	5.3	3.5	NNE	.1
82			2							2	4.2	3.5	N	.3
83										0	4.6	2.8	N	0
84			6							6	3.5	4.2	N	.8
85										0	3.5	1.4	N	0
86										0	8.8	2.8	N	0
87			1							1	3.5	2.1	N	.2
88										0	4.2	3.5	N	0
89	5			30			1			38	7.0	1.1	N	4.7
90	10	8	1	170			3			197	7.0	1.8	N	22.4
91	5	6								11	7.0	1.8	N	1.3
92	5									5	7.0	0	N	.7
93	25	20								45	7.4	.7	N	5.6
94	150									150	9.5	2.1	N	12.9
95	1000									1000	7.0	2.1	N	108.8
96	1000								1	1001	8.4	0	N	119.2
97	260	1		12	7					281	7.0	3.5	N	27.3
98	260						9			271	8.4	2.1	N	25.8
99	27									27	9.8	.7	N	2.6
100	50				1					51	8.4	1.1	N	5.4
101	8									8	9.1	1.4	N	.8
102	8						9	1		18	9.8	.7	N	1.7
103							11		1	12	9.1	1.1	N	1.2
104										0	8.8	.7	N	0
105							1			1	7.0	1.8	N	.1
106										1	7.7	1.8	N	.1
107										1	7.0	1.8	N	.1
108										0	6.3	2.8	N	0
109					1		3			4	6.0	1.8	N	.5
110										0	5.3	3.5	N	0
111										3	4.8	1.8	N	.5
112										0	9.5	1.1	N	0
113										0	6.0	1.4	NNW	0
114										0	6.3	1.8	NNW	0
115										0	7.0	1.4	NNW	0
116		4					14		1	19	8.1	1.8	NNW	1.9
117					12	6				28	7.0	0	NNW	4.0
119										0	5.5	0	NNW	0
120										0	5.3	0	NNW	0
122										0	4.2	0	NNW	0
124										0	5.3	0	N	0
125										0	3.5	3.5	N	0
127										0	5.3	.4	SSW	0
128										0	5.6	0	SSW	0
129										0	5.6	0	S	0
130										0	5.3	1.1	S	0
131										0	3.9	.4	SSE	0
132										0	3.5	1.1	SSE	0
138										0	4.6	.4	SSE	0
156										0	4.8	.7	S	0
157										0	3.9	2.5	S	0
158										0	2.8	1.4	S	0
159										0	2.6	1.4	S	0
161										0	3.2	2.8	NE	0
162										0	0	4.2	NE	0
163										0	4.2	1.8	NE	0
164										0	2.2	2.0	NE	0
176										0	1.8	2.8	NE	0
177										0	.7	3.5	NE	0
178										0	1.0	3.0	NE	0
179										0	1.8	2.8	NE	0
180										0	2.0	2.6	NE	0
181										0	3.2	1.4	NE	0
182										0	3.0	1.6	NE	0
257										0	3.2	2.1	SE	0
258							4			4	3.8	2.1	SE	.7
259							6			6	5.1	2.1	SE	.8
260							1			1	5.3	2.5	SE	.1
261							1			2	6.0	2.8	SE	.2
262							2		1	3	6.3	2.8	SE	.3
263										0	5.6	1.8	ESE	0
264									1	1	5.0	1.2	ESE	.1
273							12			12	5.0	0	W	2.4
274										0	6.3	0	W	0
275										0	5.3	0	W	0
276										0	5.0	0	W	0
295										0	0	4.0	W	0
296										0	0	4.2	WSW	0
319										0	3.9	1.8	SW	0
320										5	3.0	2.1	SW	1.0
328		20								20	1.8	3.0	N	4.2
329										0	1.8	5.2	N	0
330										0	1.9	5.0	N	0
331		40								40	2.8	3.9	N	6.0
332										0	3.0	3.5	N	0
333										0	4.6	2.1	N	0
334		8								8	3.0	1.9	N	1.6
342										0	3.5	.8	S	0
343										0	5.3	1.4	S	0
344									1	3	5.4	1.4	S	.4
345										2	5.6	1.4	S	.3
346										0	5.5	1.8	S	0
348										0	2.0	2.1	S	0
349										0	4.2	1.3	S	0
350										0	4.0	1.1	S	0
357										0	4.3	.5	WNW	0
358										0	4.5	.9	WNW	0
359										0	5.3	0	WNW	0
360										0	5.4	0	WNW	0
361										0	3.8	1.0	WNW	0
362										0	3.5	1.1	WNW	0

Table I—Continued

Divisions	*Lonchopria*	*Belopria*	*A. diversipennis*	*A. sparsilis*	*P. cyanomelas*	*P. divaricatus*	*C. rhytidophorus*	*Paratetrapedia*	*Thygater*	Total nests	m² layer C_2	m² layer C_1	Exposure	Total nests/m²
379										0	3.6	1.6	ESE	0
380										0	3.8	1.8	ESE	0
381										0	5.6	1.8	ESE	0
382										0	5.8	1.8	ESE	0
383										0	7.0	.5	ESE	0
384										0	7.0	.4	ESE	0
385										0	5.9	0	ESE	0
386										0	5.6	0	ESE	0
409										0	3.5	2.0	SSW	0
410										0	3.5	1.8	SSW	0
411						1				1	3.5	2.1	SSW	.3
412						1				1	3.8	2.0	SSW	.2
413						1			1	2	6.0	1.4	SSW	.3
414						1				1	6.6	1.0	SSW	.1
415								1		2	8.1	0	SSW	.2
416										0	8.0	0	SSW	0
417									1	2	7.0	0	SSW	.3
418										0	7.0	0	SSW	0
419										0	6.6	0	SSW	0
420										0	6.8	0	SSW	0
421										0	8.0	.7	S	0
422										0	8.1	.9	S	0
423										0	6.0	1.6	S	0
424										0	6.5	1.8	S	0
425										0	7.0	1.8	S	0
426										0	7.0	1.4	S	0
427										0	5.3	3.2	S	0
428										0	5.5	4.2	S	0
429										0	7.1	2.5	S	0
430								1		1	7.5	2.1	S	.1
431										0	7.7	2.1	S	0
432										0	7.7	2.2	S	0
433										0	5.6	2.4	S	0
434										0	5.9	2.6	S	0
435										0	8.0	2.8	S	0
436										0	8.4	2.6	S	0
437										0	8.7	1.8	S	0
438										0	8.9	1.8	S	0
439										0	9.5	2.1	S	0
440										0	9.5	1.8	S	0
441										0	8.5	1.4	S	0
442										0	8.3	1.1	S	0
443										0	7.7	1.1	S	0
444										0	7.5	1.4	S	0
445										1	7.1	1.6	S	.1
446										0	6.9	1.8	S	0
447										0	5.3	1.1	SSW	0
448										0	5.3	1.1	SSW	0
449			30							30	5.3	1.4	SSW	4.5
450			45							45	4.2	3.9	SSW	5.6
451			360						1	361	1.1	5.3	SSW	56.4
452			13							13	0	7.0	SSW	1.9
453			13							13	1.6	2.5	SSW	3.2
455										0	2.1	2.4	SSW	0
456										0	2.0	2.6	SSW	0
457										0	1.8	3.0	SSW	0
458										0	1.9	3.5	SSW	0
459										0	3.5	2.1	SSW	0
460										0	4.6	2.5	SSW	0
461										0	6.8	.6	ENE	0
462										0	7.0	.4	ENE	0
463										0	4.3	2.9	ENE	0
464									1	1	4.1	3.5	ENE	.1
465									2	2	3.5	3.5	ENE	.3
466										0	3.5	3.0	ENE	0
467									1	2	3.5	1.8	ENE	.4
468										0	3.9	1.1	ENE	0
469										0	4.1	.7	ENE	0
470										0	4.3	.9	ENE	0
471										0	5.1	1.5	ENE	0

Table I—Continued

Divisions	*Lonchopria*	*Belopria*	*A. diversipennis*	*A. sparsilis*	*P. cyanomelas*	*P. divaricatus*	*C. rhytidophorus*	*Paratetrapedia*	*Thygater*	Total nests	m² layer C_2	m² layer C_1	Exposure	Total nests/m²
472										0	5.3	1.7	ENE	0
473										0	7.0	0	ENE	0
474										0	7.0	0	ENE	0
475										0	7.0	0	ENE	0
476										0	7.0	0	ENE	0
477									1	1	7.0	0	ENE	.1
478										0	7.0	0	ENE	0
479										0	7.6	0	ENE	0
480										1	7.7	0	ENE	.1
481			1						1	3	7.5	0	ENE	.4
482									4	4	7.3	0	ENE	.5
483										1	8.5	0	ENE	.1
484										0	8.9	0	ENE	0
485			1						1	2	8.2	.9	ENE	.2
486										0	8.0	1.4	ENE	0
487									1	1	3.9	2.8	ENE	0
488									1	1	3.5	2.2	ENE	.2
489										0	3.5	1.4	ENE	0
490										0	3.5	1.0	ENE	0
491									1	1	3.3	1.0	ENE	.2
Totals	2813	107	478	212	21	125	78	26	25	3928	1212.5	378.9		

0.062 to 2 mm; silt, 0.004 to 0.062; and clay, less than 0.004. Hardness was determined *in situ*, using a chisel dynamometer (type of I. F. Golubev) to measure resistance to penetration in kilograms of pressure. The determinations of pH were made with a Beckman pH meter using mixtures of half water and half soil allowed to stand for 24 hours. Humidity, expressed as percentage (by weight) of water in the soil, was determined from small samples removed by a sampler from a depth of about 20 cm in the bank, carried to the laboratory in closed metal containers, weighed, dried in an oven at 105°C for a minimum of two hours and reweighed. It was determined that more time at the same temperature did not result in further weight reduction. As not all the humidity determinations could be made on the same day, they were made on three different days of similar weather, the determinations made on any one day being similarly marked in the last column of the table. To show what reliance can be placed on these data, samples from the immediate vicinity of sample 1 were determined on each of the three days. Average percentages, based on samples from divisions 89-96, for the three days were 16.7+, 17.0*, and 19.5°; the marks after these figures correspond to those in the last column of Table II.

DISCUSSION

The tables and figures in the preceding part of this paper present most of the data available to us regarding the distribution of bees' nests in the

TABLE II. Physical factors determined for soil samples (for explanation, see text)

Sample (Fig. 2)	Division (Fig. 1)	Soil Horizon	PARTICLE SIZE (%) (1) pebbles	(2) sand	(3) silt	(4) clay	(5) Hardness	(6) pH	(7) Humidity
3	89	B	5.0	26.0	27.0	42.0	20	5.65	18^*
1	89	C_2	.6	43.5	49.5	6.5	30^+	5.68	15^* 17 19°
2	89	C_1	.7	26.3	43.0	29.0	16	5.40	18^*
4	89	C_2	0	44.0	47.0	9.0	30+	5.70	14^+
5	89	C_1-C_2	21.0	24.6	44.9	9.5	17	6.05	12^+
6	89	C_1	0	10.0	53.0	37.0	20	5.90	23^+
7	89	C_2	.3	11.9	73.0	15.0	30+	5.68	17^+
8	90	C_2	2.8	26.2	56.5	14.5	30+	5.70	23^+
9	90	C_2	1.0	28.5	52.5	18.0	30+	5.85	16^+
10	90	C_2	0	37.0	52.0	11.0	30+	5.75	16^+
11	90	C_2	3.5	23.5	60.0	13.0	30+	5.88	12^+
12	90	C_1	4.6	23.4	46.0	26.0	30	5.95	14°
13	95	C_2	.7	36.3	50.0	13.0	30+	5.20	20°
14	95	C_1	8.0	29.0	39.0	24.0	21	5.95	16°
15	95	C_2	1.2	32.8	50.0	16.0	26	5.45	11°
16	95	C_1	.4	39.6	36.0	24.0	..	....	21°
17	96	C_2	0	19.0	70.0	11.0	28	5.98	23°
18	96	C_2	2.8	16.2	68.0	13.0	..	5.65	14°
19	96	C_1	6.0	19.0	44.0	31.0	18	5.82	14°
20	96	C_2	2.2	20.8	67.0	10.0	..	5.58	20°
21	96	C_1	6.3	23.7	33.0	36.0	16	5.70	24°
22	404	C_2	7.4	22.6	50.0	20.0	21	....	14°
23	436	C_2	10.0	20.0	65.0	5.0	19	....	20°
24	450	C_1	4.0	31.0	35.0	30.0	8	....	33°
25	450	C_1	....	....	....	....	14	....	24°
26	450	C_1	2.4	19.6	45.0	33.0	18		
27	449	C_1	.6	10.9	67.5	21.0	16		
28	450	C_2					26		
29	449	C_1					21		

banks. Various factors affecting them are discussed here.

1. *Steepness of soil surfaces.* As the banks are nearly the same (subvertical) in this respect, no important data were obtained regarding this factor. No special situations were found in the few areas of sloping ground. However, the association of bees found in the banks is different from that found in flat ground. Of the bees listed above, we found only *Paroxystoglossa* also in flat ground.

2. *Irregularities of surfaces.* We noted a strong tendency for *Thygater* to start its burrows in preexisting depressions or under small overhangs, or in cavities where we had previously excavated nests, almost anywhere on the banks. *Lonchopria* also tends to start burrows within cavities in the bank, so that within the nesting area of this bee, dense concentrations of nests occurred in cavities which we had excavated, although the vast majority of the nests entered the plane bank face.

3. *Exposure to the sun.* The above described behavior of *Thygater* and *Lonchopria* may be related to insolation, as may also the fact that all nests of *Neocorynura* and *Bicolletes* were found in the shade under an overhang. Of more general interest is the fact that there are great differences in the abundance of nests in banks which must be pedologically alike on opposite sides of a road. Such banks must differ only in insolation and related phenomena. We had expected to find humidity quite different in banks on the two sides of the road, but samples 22 and 23 (Table II), taken from a bank facing almost south and hence shaded, do not show a higher humidity than many samples (numbers 1 to 21) from apparently identical soil on the north-facing sunny bank across the road. Hence we assume that insolation makes its effect felt through temperature of the soil, of the soil surface, or of the adjacent air. Possibly none of these things is involved, but merely the fact that bees fly more readily or can locate nests or suitable nesting sites more readily in the sun than in the shade. In any case, in order to assemble our data on the importance of exposure, Table III was prepared. The 360° of the compass were divided into the 16 sectors shown in the first column (indicated by SW, southwest; WSW, west southwest, etc.) Divisions of the banks were grouped according to the direction of a line perpendicular to the bank face of each division, and the number of square meters of suitable soil (layers C_1 and C_2) facing each direction is shown in the second column of Table III. Finally, the number of nests per square meter of such soil in each sector is shown in the third column, and the same, independently calculated for four large sectors, appears in the fourth column.

TABLE III. Relation between exposure of banks and abundance of bee nests. (For explanation, see text; suitable soil is indicated only when in quantities of over 4 square meters per division.)

Exposure	Suitable soil (C) in m²	Nests/m²	Nests/m²
SW	10.8	.46	.24
WSW	4.2	0	
W	25.6	.47	
WNW	30.3	0	
NW	0		5.35
NNW	55.9	.66	
N	420.9	7.61	
NNE	156.1	.93	
NE	52.6	0	.07
ENE	210.2	.10	
E	9.6	.10	
ESE	65.8	.02	
SE	44.1	.36	.87
SSE	13.9	0	
S	327.0	.02	
SSW	169.1	2.79	

It is clear that more data would be desirable, since banks facing in certain directions are limited or even absent. Nevertheless, it is apparent that nests are relatively abundant in banks facing approximately north, toward the midday sun. This generalization applies to all the common species except *Augochloropsis diversipennis* and is especially striking when apparently identical banks on the two sides of an east-west road are compared. (In Table I, compare the numbers of bees' nests in north-facing divisions 69 to 110 with those in divisions 156 to 159 and 409 to 420 on the opposite side of the road.) The only exception to these statements is the abundance of nests facing south southwest and is due entirely to an aggregation of *Augochloropsis diversipennis* in an exceptional local area of deep, unusually soft soil of layer C_1 resulting from soil creep. In layer C_2 this same bee showed the usual distribution, most of the nests facing more or less north. If we are right in attributing this nest aggregation to a local soil condition, it indicates that for this species, unusually favorable soil can, at least in part, counteract the influence of presumably unfavorable exposure.

4. *Soil.* Edaphic factors are obviously very important in determining distribution of nests. To illustrate this, we need only cite the facts, previously stated, that all the nests of *Melitoma* which we found were in illuvial soil (B), while most of the other nests were in decomposed gneiss (C). Long sections of bank which lacked exposures of layers C_1 and C_2 contained no bee nests. This may be due to the fact that the eluvial and illuvial soils crack extensively, break easily, and present very hard dry surfaces (in spite of relatively low hardness as determined by chisel dynamometer and shown in Table II). These characteristics may be due to the relatively high percentage of clay present in these more superficial layers, as shown in Table II.

Within the decomposed gneiss (layer C) the distribution of nests of some species is strikingly patchy, even in sections of straight bank similarly exposed to the sun. This patchiness can easily be noted by running down the columns of Table I. Nest aggregations can be noted there for all species except *Thygater,* which is very much scattered. We have seen a bank rather densely inhabited by *Thygater analis* in Curitiba, and a much greater aggregation has been recorded by Bertoni and Schrottky (1910, 1911), but at least the one we observed was where only a very limited bank face was available to the bees. *Chloralictus rhytidophorus* was widely scattered with a number of isolated nests (and probably many more existed), but with several small aggregations. *Augochloropsis diversipennis* also had isolated nests but there was one large aggregation already mentioned which might be explained by a local area of particularly deep, soft, moist soil (see sample 24, Table II) containing pieces of less decomposed gneiss (like layer C_2) due to soil creep. Each of the other species listed in Table I had nests in one to several aggregations, although some also had a few isolated nests. Only in the case of *Augochloropsis diversipennis* could an aggregation be tentatively attributed to an obvious pedological feature.

Figure 2 and Table II were prepared in an effort to obtain more information that might explain these aggregations. The portion of the bank (divisions 89-96) involved in this more detailed study is straight; there are no factors of steepness, surface irregularities, or exposure that could explain the nest aggregations. Kruskal-Wallis tests (nonparametric analyses equivalent to analyses of variance, see Siegel, 1956) were made with data shown in columns numbered 1 to 5 and 7 of Table II, thanks to Dr. Robert R. Sokal of the Department of Entomology, University of Kansas. Soil characteristics of three groups of samples (1, 2, outside nesting areas; 4 to 12, in area of *Augochloropsis sparsilis;* and 13 to 21, in area of *Lonchopria*) were compared. These analyses yielded χ^2 results which test the hypotheses that the three groups were selected from the same population of samples or from populations identical with respect to averages. None of the χ^2 values (range, 0.56 to 3.10) were of such a magnitude as to warrant rejection of the hypothesis. Expressed biologically, this verifies the assumption that *particle size, hardness,* and *humidity,* as they varied in layers C_1 and C_2 in the divisions indicated in Figure 2, where not responsible for the nest aggregations observed in those zones. A one way analysis of variance indicated that there were no significant differences in pH (F value of 2.53) among the three groups of samples. *Hardness,* as we measured it, is greater in lower layers of soil (although, as stated above, surface hardness seems much greater in layers A_2 and B), but is not correlated with nest aggregations. Thus samples 1 and 2, outside any nesting area, were neither harder nor softer than samples 4 to 12 from corresponding layers in the nesting area of *Augochloropsis sparsilis,* nor than samples 13 to 21 from corresponding layers in the area of *Lonchopria.* Particle size averages less in upper layers than lower, as is particularly evident on examining the column headed "clay" in Table II. Perhaps this is the reason for the correlated variation in hardness. As with hardness, there is no correlation between particle size and nesting areas within layers C_1 and C_2.

Layer C_2, because of retention of gneissic structure, is full of sheets and patches of different color, consistency, particle size, and no doubt chemical nature. Thus, there are white, orange, yellowish brown, and purplish patches in a generally red background. The matter was studied particularly in the area of *Augochloropsis sparsilis* (division 90, Figure 2). Some small areas (sample 5, Table II) are so full of pebbles that it seems unlikely that the bees could use a bank made entirely of such material, and although nests sometimes enter such areas, they were not found made entirely within such material. Otherwise, location of nests seemed to be quite independent of the above mentioned variations within the decomposed gneiss. To exemplify this, we need only mention that this bee normally lines its cells with soil taken from another part of the nest. Because some of the nests are partly in soil of one color and partly in another, we have found the cells of successful nests constructed in red soil but lined with pure white clay, others in brown material but lined with red, etc. Also, entire successful nests have been found within patches of all the colors and consistencies of the decomposed gneiss except white and purplish (which are very limited in extent) and the coarse-grained patches already mentioned. We can only conclude that these local variations within the gneiss (except the coarse-grained patches) are of no importance in determining nest location.

5. *Internal Behavioral Factors:* We are left with no physical factors known to us which might explain most of the nest aggregations, for example those shown in Figure 2. We conclude, therefore, that the aggregations probably result from a tendency (of variable strength in different species) to form aggregations regardless of an extensive and physically suitable nesting area. This is most easily visualized as a tendency for young female bees from one nest to return to the vicinity of that nest to construct new nests. This is the mechanism suggested by Malyshev (1926) to explain aggregations of nests of *Andrena vaga* in Russia.

One might expect selective factors to operate against aggregative behavior. For example parasites and predators of bees could presumably more easily find their hosts if aggregated than if dispersed. If we are correct, more powerful selective factors favoring aggregative behavior must exist for some species. Ease of finding mates, so that females can mate and start nesting activities while still young, may be one factor favoring aggregations. A factor that may have been important in the establishment of aggregative behavior is the possibly very limited suitable bank space available under primitive conditions. Perhaps the bees were forced together by lack of space, and retain this behavior even when more space is available. On the other hand, various bees which nest in flat ground also form aggregations.

Conclusions

It is evident that various environmental factors such as steepness of surface, exposure, and soil, are of great importance in determining nesting sites of bees, and that surface irregularities of the soil are of minor importance. Within one soil layer, minor variations in humidity, pH, hardness, particle size, and color were apparently not correlated with selection of nesting sites in the majority of cases. Some bees (*e.g. Thygater analis*) seem to distribute their nests throughout suitably exposed soil of the appropriate type, so that in the banks which we studied, there were no aggregations. Other bees (*e.g. Augochloropsis sparsilis, Lonchopria cingulata*) construct nests in aggregations, even in straight and apparently uniform banks. Studies of soils within and outside of these aggregations showed no consistent differences. It is therefore probable that the aggregations result from a tendency on the part of the bees to locate nests in groups even in the presence of extensive suitable nesting areas. Perhaps aggregations result from a tendency for young bees to return to the vicinity of their parental nest to construct new nests.

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Further acknowledgments appear in footnote no. 1.

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POPULATION CONSEQUENCES OF A SUSTAINED YIELD PROGRAM FOR NORWAY RATS

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PART I

This paper explores the consequences of removal from a population at regular intervals of the number of rats that theoretically should give a sustained yield. A sustained yield is the number (or weight) of individuals that may be removed from the population and permit the population to remain at a designated level. While the yield may be designed to keep the population at any level, usually the maximum sustained yield is desired. For economically valuable species a sustained yield is desirable because it provides a stable and predictable supply and economic return and employment. But for pest species a sustained yield is undesirable for it means an unending control program.

To study the characteristics of yield, Norway Rats (*Rattus norvegicus*) in three residential blocks in Baltimore were used. The rats lived in back yards, garages and a few basements. The population characteristics have been described (Davis 1953). The population numbers were estimated by a sign-survey method which permits the detection of changes as small as 20 percent (Davis and Christian 1956). For this experiment the yield was calculated on the assumption that the populations were following a logistic equation (see Part II). For each block the constants of the equation were determined and the rate of change per month determined for the estimated inflection point. The lower asymptote was determined as well as the upper (Table I). The maximum sustained yield is equivalent to the slope at the inflection point because removing the increase should permit the population to remain at that point. Thus the maximum sustained yield for the blocks was calculated to be 10.1, 10.2 and 7.5 rats per month.

Usually a sustained yield program consists of removing a specified number of animals during a time period. Thus if 10 rats are to be removed each month, then one rat should be removed every third day. For practical reasons it is obviously impossible to trap the rats at such precise intervals. Hence rats were trapped once a month for a period necessary to catch the quota. Also for practical reasons it was decided that it was better to trap the population back to a level each month than to remove a particular number each month. Thus, instead of finding out what happens to the

TABLE I. Population constants for three blocks

	Block Number		
	140111	140134	140201
Population at upper asymptote (K+C)	202	140	115
Population at lower asymptote (C)....	22	0	34
Population at inflection point C+K/2.	112	70	75
Slope at inflection dy/dt per month...	10.1	10.2	7.5
Trap down monthly to population....	107	65	69

TABLE II. History of population in three blocks

	Block Number			Mature Females	Percent Pregnant
	140111	140134	140201		
Population in Feb., 1954.	152	130	130		
Removed in March, 1954.	73	48	57	79	30.2
Population April, 1954...	100	70	80		
Census (and removed)					
April.............	99(0)	70(5)	85(16)	62	32.2
May..............	120(13)	105(23)	100(30)		
June..............	120(11)	90(15)	80(14)		
July..............	125(15)	85(11)	75(8)	25	16.0
August...........	98(0)	100(14)	80(17)		
September.........	120(13)	90(21)	80(11)	33	33.3
October...........	130(8)	66(0)	75(5)		
November.........	160(6)	60(6)	45(6)		
December.........	....	67(6)	53(6)	18	16.7
January...........	....	65(6)	60(5)		
February..........	....	60(6)	55(5)		
March............	....	55	46		
Number predicted					
(April-September)...	50.5*	61.2	45.0		
Actually removed...	52*	89	96		

*Only May-September.

population when a particular number is removed, this paper reports what happened to the yield when the population was kept at a particular level. Each month, therefore, a number of rats was removed from each block to bring the population down to a number one half of the calculated yield below the estimated inflection point. For example, from Table I, in Block 140111 half of the yield was 5 rats and the population at the estimated inflection point was 112 rats. In May the population was estimated to be 120 rats and, therefore 13 rats were removed to bring the population down to 107 rats.

It should be noted that the results are not as exact as the figures might suggest. The population estimates have an error such that Block 140111 in May may have had as few as 108 rats or as many as 132 rats. Also it was not always possible to remove the exact number of rats and practical problems such as vandalism resulted in death or loss of additional rats. In Block 140134 it was usually impossible to catch the quota for each month and thus the population remained above the inflection point.

In March, 1954, after two years of observation the population in each of these three blocks was approaching the upper asymptote and was trapped down to the inflection point. The history of each block is given in Table II and shown in Figure 1. Naturally the age and sex composition of the rats is important in the results. The sex and weight (3 size-classes) composition of the rats from each block was determined as percentages of the total removed in March from each block. Then each month a "quota" was established that was as near as possible to the percentages for the block. For example, in May in Block 140111, the quota to be removed was 13 rats and was set up thus for the males: 1 or 2 less than 200 grams; 3 or 4 between 200-400 grams; and 2 or 3 more than 400 grams. Actually in the trapping period 3 small, 3 medium and one large male were caught. Although the departures from the quota of removals were large in almost every trapping period, the system prevented excessive departures from the desired proportion, for in some months as many as a dozen rats were released because they exceeded the quota. The detailed figures are not presented here. It will be noted that the proportional make-up of the quota was based on the age composition of increasing populations that were approaching the asymptote whereas it should have been based on the composition at the estimated inflection point which occurred in the preceding fall. Unfortunately no reliable method for determining the composition without altering the population is available.

The three populations (Table II) produced one and a half times as many rats as had been calculated by the method used for a sustained yield during the period of trapping. However, it cannot be said whether the differences between predicted and actual removal rates are in fact real or merely a caprice of sampling because no standard errors are available. The history of each block (Figure 1) may be summarized. Block 140111 was producing a few more rats than predicted until August when there was a decrease in population. In September 1954 the quota trapping was stopped because it was desired to see if the block would increase again as it had in the previous September. Therefore, after August only samples for studies of adrenals were removed. (That the adrenal sample in September was numerically the same as the quota was pure coincidence.) It will be noted that the population rapidly increased to 160. Unfortunately for our

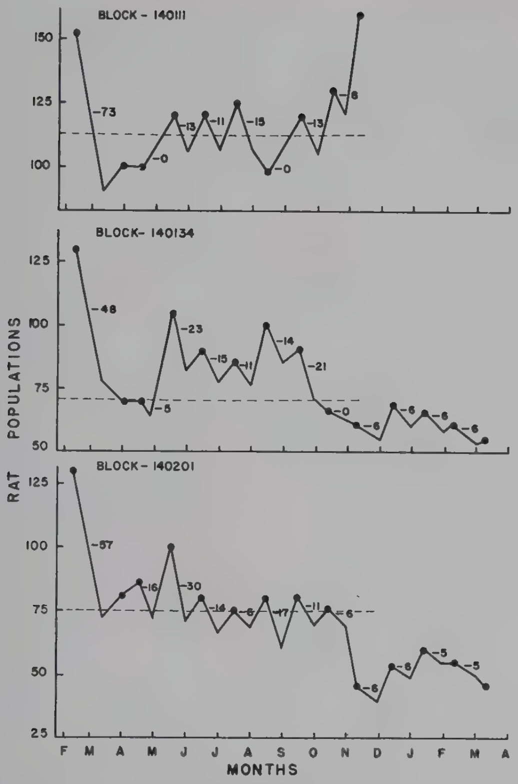

FIG. 1. The history of 3 populations of rats in blocks trapped monthly. The dotted line is the level for maximum sustained field.

purposes, the experiment was ended in December when housing rehabilitation altered the habitat so much that the population declined to 80 in three months.

Blocks 140134 and 140201 had essentially the same history. Each produced more rats than predicted until September when the populations dropped drastically and remained low from October to March. The reason for the decline is not known. No major change in habitat was apparent. Since the autumn is a season of high reproduction, breeding should have continued. However, it became increasingly difficult to catch the large rats that were necessary to fulfill the quota but excess numbers of small rats were caught. It is possible that a shift in age composition occurred that reduced the average age to such a low level that reproduction was drastically reduced. Unfortunately methods of testing this aspect are not available since one cannot determine the true size and sex composition for the population in a block but only the "trappable" portion. Another possible explanation is that the constant removal of rats prevented the establishment of a social system that would permit adequate reproduction. It will be noted that trapping failed to reduce the population adequately in block 140134 thereby reducing the theoretical yield slightly from 10.2 rats. Rats were removed even after the population had drastically declined in order to examine the adrenals rather than to continue the sustained yield aspects.

The reproductive pattern of the rats during this year showed no striking differences from that of a normal population. Davis (1953) showed that about 19 percent of the mature (vaginal orifice perforated) females in a stationary population were pregnant while 30 percent in an increasing population were pregnant. Table II gives the figures for percent pregnant at various times. The fact that 30 percent of 79 mature females were pregnant in March 1954, agrees with the population history to indicate an increasing population. The pregnancy level continued high during the spring breeding season, dropped as usual in summer, rose for the fall breeding peak, and then dropped as usual to a winter level (16.7 percent) that is indistinguishable from the percentage (21.4 percent) in 122 rats taken during the past 6 years in winter from 10 increasing populations.

The fact that the population maintained the normal proportion of pregnancies suggests that the collapse of the population was not due to reduction of pregnancy. However, the age at first pregnancy may have declined so that, while the proportion pregnant remained the same, the age decreased until the physiological limit was reached and the proportion of mature females in the population eventually became very small. Unfortunately our data are not suitable for testing this point. The number of embryos per female was 10.3 in the March sample and 9.3 in the sustained yield samples but the difference is not significant ($p = .16$).

The changes in size of the adrenal glands were described in detail (Christian and Davis 1955). In summary the adrenals decreased in size by a third when the population was reduced to the sustained yield level and then remained thus for several months. However, a gradual increase in size occurred after September, perhaps in part due to environmental changes in the blocks.

DISCUSSION

The rat populations in these three blocks showed peculiar responses to the sustained yield program. At first the yield was high and then the population collapsed. Apparently the population mechanisms are extremely complex. A number of points can be suggested. (1) A *reduced* population may not increase in the same manner as an increasing population. If this is true, then the yield cannot be predicted from the logistic (or some other equation) but must be worked out empirically from experiments on reduced populations. (2) The constant removal of individuals may increase the reproductive rate, perhaps by lowering the age at first pregnancy. (3) Removal may disrupt the social organization.

The collapse of a population under sustained yield has been recorded several times for fish (Fitch 1953; Miller 1949) and whales (Hjort *et al.* 1933). In these cases the average age of the females was so reduced that reproduction was reduced. However, in the rat populations here described this situation may not have occurred. Reproduction at all times was essentially normal for the season and at a high level in terms of percent of mature females that were pregnant. However, the decline may merely be due to the absolute number of mature females that were present. This possibility requires examination.

The sudden decline in the populations of the two blocks in October and November, of course, might be due to some mortality factor but none was apparent.

In concluding these comments about possible explanations for the failure of the program to follow the predictions, it seems pertinent to suggest that in a sustained yield program the age composition must be carefully examined and may be the key to success.

PART II

The maximum size of each rat population used in these experiments was estimated by fitting a logistic curve to the data for each block. The basic assumption necessary to do this is that the growth of the rat population follows a logistic curve. The logistic has been shown to be reasonably good fit for the growth of many populations and data for rat populations (Emlen *et al.* 1948) suggest that the logistic may fit for this species. The equation for the logistic curve is $y = \frac{K}{1+e^{a-bx}}$ where y = growing mass, x = time, K is the upper limiting value or asymptote, and a is a constant of integration defining the relative position of the origin and the curve. It may be necessary to use a lower asymptote as well, C, to represent the population when increase started. Then the logistic becomes $y = \frac{K}{1+e^{a-bx}} + C$.

The constant K (and C if it was used) was determined by trial and error beginning with reasonable estimates for the values based on the histories of the populations. An account of the process we used to fit a logistic to population data is given below, using the rat population from Block 140134 in the present experiment as an illustrative example.

The first step is to convert the logistic to a linear function.

$y = \frac{K}{1+e^{a-bx}}$ reduces to an equation of a straight line:

$$a \log e - x\,(b \log e) = \log \frac{K-y}{y} \qquad (1)$$

$$\text{or } A - Bx = W \qquad (1')$$

where:

$A = a \log e$
$B = b \log e$
$W = \log \frac{K-y}{y}$

or, if a lower asymptote is used,

$$\log \left(\frac{K-y+C}{y-C} = W'\right)$$

TABLE III. Data for rat population from block 140134. K estimated to be = 140, C = 0

Date	x	y	K-y	$\frac{\text{K-y}}{\text{y}}$	W
17, Apr. 1952...	1	2	138	69.0	1.839
13, Oct. 1952...	7	10	130	13.0	1.114
27, May 1952...	14	62	78	1.26	0.100
15, Sept. 1953..	18	88	52	0.59	9.770-10
17, Nov. 1953..	20	115	25	0.22	9.342-10
21, Dec. 1953...	21	115	25	0.22	9.342-10
28, Jan. 1954...	22	130	10	0.13	9.114-10
27, Feb. 1954...	23	130	10	0.13	9.114-10

The next step in this method of fitting a logistic to actual data is to obtain the best values of K to produce a linear fit for (1). This may be done graphically. W or W' is plotted against time (Figure 2) using the experimental values for y from Table III and estimating values for K. If K is too low, the plot will curve down, whereas if K is too high, the plot will turn up. K values are tried and W recalculated until a reasonable linear fit is obtained for W against x (time). In this case a K value of 140 gave the best result. If a lower asymptote (C) is used, various values of both C and K must be tried until the best straight line is obtained. To reduce the extent of calculations it is worthwhile to use semilog paper and plot $\frac{K-y}{y}$ against x.

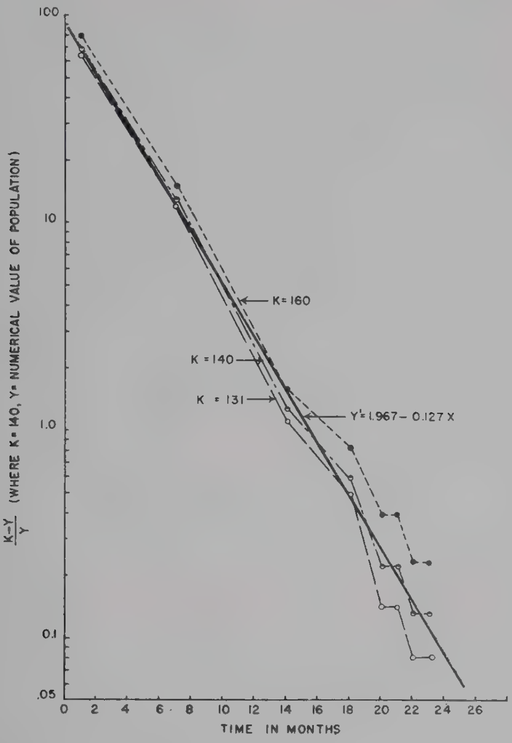

FIG. 2. A plot of population against time for block 140134 demonstrating method of finding a value for K.

Next, having approximated a value for K, a regression was obtained by the method of least squares for the values of W on x. In the case of Block 140134 the equation was:

$$W = 1.967 - (0.127)\,x \qquad (2)$$

Therefore plotting W (or W') against x is the linear function $A + Bx$, where B is the slope of line, A is the intercept on the ordinate, and $x =$ time.

In using the reduction equation ($1'$) to obtain the theoretical values of the logistic curve, it is noted that ($1'$) gives only a transform of the original y, this transform is, of course, W. For example, when we substitute W for $\log \frac{K-y}{y}$ then $\text{antilog } W = \frac{K-y}{y}, = \frac{K}{y} - \frac{y}{y} = \frac{K}{y} - 1,$

$$(\text{Antilog } W) + 1 = \frac{K}{y} \text{ so } y = \frac{K}{(\text{antilog } W) + 1} \qquad (3)$$

Values for y may be found from (3) using equation (2) to obtain values of $\frac{K-y}{y}$ for various values of x.

The point of inflection of the logistic is at $\frac{K}{2}$ (or $\frac{K}{2} + C$), at which point $\frac{dy}{dx}$ (infl.) $= \frac{Kb}{4}$. The rate of increase in terms of rats per unit time, in this month, is obtained by $\frac{KB}{(4)\ (0.434)}$ or $\frac{Kb}{4}$.

For the rat population in Block 140134, the point of inflection with $C = 0$ is $K/2$ or 70 rats; $\frac{dy}{dx}$ (infl.) $= \frac{KB}{(4)\ (0.434)} = 10.2$ rats per month.

The maximum sustained yield was based on these calculations. The rat population of Block 140134 (Figure 3) theoretically should have been trapped back to 70 rats and then 10.2 (or 10) rats uper month removed thereafter.

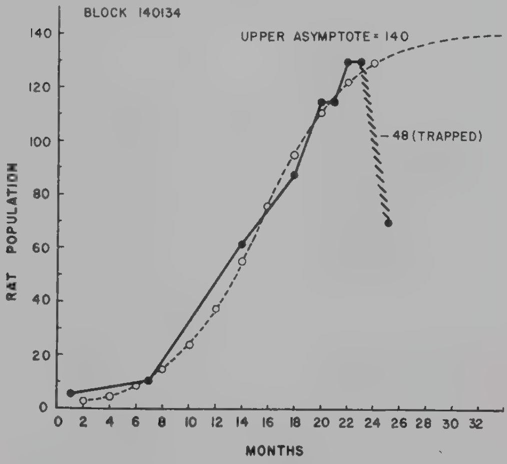

FIG. 3. The observed populations (solid line) and the population (dotted line) calculated from the logistic for block 140134.

Logistics were fitted in similar fashion and the values for $\frac{K}{2}$ and $\frac{dy}{dx}$ (infl.) calculated for the other 2 blocks in this experiment.

SUMMARY

To enlarge our understanding of population mechanisms a program of sustained yield was conducted on Norway Rats (*Rattus norvegicus*) in three blocks in Baltimore. From the history of the increase in the rat population, the inflection point of a logistic was calculated. The populations were then reduced to their inflection points and kept there from April to August or October. During this time it was necessary to remove about 1.5 times as many rats as predicted from the rate of increase at the inflection point. Removal of rats was ended in one block in August and the population returned to a high level. The pop-

ulations in the other blocks collapsed in October. During all this time the percentage pregnant was normal for increasing populations. Presumably the collapse of the populations resulted from a decline in average age of females till they were too young to breed so that while the percentage of sexually mature females breeding remained high, the number of mature females dropped drastically. A second part describes the procedure used here in fitting the data to a logistic curve.

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MORTALITY OF OVERSTORY TREMBLING ASPEN IN RELATION TO OUTBREAKS OF THE FOREST TENT CATERPILLAR AND THE SPRUCE BUDWORM[1]

A. W. GHENT[2]

INTRODUCTION

During the period 1940-1949, the Lake Nipigon forest area of Ontario was devastated by a severe outbreak of the spruce budworm, *Choristoneura fumiferana* (Clem.). This outbreak began on the west shore of Lake Nipigon, a large lake about 35 miles north of Lake Superior. The area of the outbreak increased each year until, by 1948, balsam fir trees, *Abies balsamea* (L.) Mill., had been heavily defoliated over an area approximately 160 miles from east to west, and 100 to 120 miles from north to south, completely surrounding Lake Nipigon (Belyea, 1952). This area includes the forest surrounding Black Sturgeon Lake and most of that drained by the Black Sturgeon River. During the later years of the Lake Nipigon budworm outbreak, high populations of spruce budworm became evident on Sibley Peninsula, and persistent high populations on the Sibley and Black Bay peninsulas in Lake Superior have effected heavy mortality of balsam fir in recent years (Sippell *et al.* 1953, 1954, 1955).

Wellington *et al.* (1950) include the Lake Nipigon outbreak in their consideration of closely followed outbreaks of recent decades that have provided data on physical and biological indicators of spruce budworm infestations. These authors point out that the forest tent caterpillar, *Malacosoma disstria* Hbn., has regularly preceded the spruce budworm, and is therefore of value as a biological indicator of potential spruce budworm outbreaks even when their host trees are not present in the same stands. A survey of past outbreaks, which they present, indicates that population upsurges of both insects have regularly followed periods of suitable weather; tent caterpillar populations have tended to build up during years of moderately warm, cloudy, humid weather associated with periods in which a greater than average number of storm centers passed through the region of the subsequent oubreak; conversely, spruce budworm populations have tended to increase during periods of clear, dry weather associated with the passage of a smaller than average number of storm centers. Wellington *et al.* pay considerable attention to the possible role of the forest tent caterpillar as an ally of the spruce budworm. They suggest that outbreaks of the forest tent caterpillar might be related to subsequent outbreaks of the spruce budworm in several subtly different ways:

> . . . Overmature poplars become decadent, but about 20 years is required to eliminate the original stand if the trees are not attacked by tent caterpillars. On the other hand, if such trees are severely defoliated by tent caterpillars for two or three years, the period of decadence and elimination may be shortened to five to seven years. . . . Anything that hastens the succession so that conifers become dominant tends to increase the susceptibility of the stand to spruce budworm attack. If this succession occurs during the climatic fluctuation in advance of the one associated with a spruce budworm outbreak, the suceptibility

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of the area is greatly increased. If it occurs during the period of drought that frequently carries over into the early outbreak period, additional areas are opened up that would be relatively untouched otherwise, and the oubreak becomes more severe.

> The points treated above lead to some pure speculation . . . that should be kept in mind during future observations. The observed grades of susceptibility, to the spruce budworm, among stands with varying content of dominant poplar during the preoutbreak period, and the effects of exposure of host trees on population growth under suitable physical conditions, suggest that an effective exposure may occur if complete defoliation of poplar were to occur at the same time that physical conditions were changing in favor of the spruce budworm. This need not involve elimination of the poplar trees, but only temporary elimination of their foliage. . . . Removal of poplar leaves would temporarily expose overtopped large conifers in a manner that should be comparable to that produced by slower removal of whole poplar trees, and physical conditions for larvae on the conifers should more closely approximate conditions on dominant trees during the period the overtopping foliage is absent. . . .

The present study was undertaken to assess these possibilities in greater detail.

Bess (1946) and Blais (1952) have both outlined the role played by staminate-flowering balsam fir trees in outbreaks of the spruce budworm. Blais demonstrated that flowering balsam fir trees were generally larger in diameter and total height, had a greater crown length, and displayed a greater proportion of "sun" foliage than nonflowering trees. These attributes are characteristic of exposed balsam fir trees occupying dominant positions in a forest stand. It follows that such factors as the defoliation of a broad-leaved canopy or the removal of whole trees from a protective overstory, both of which would increase the dominance and exposure of intermediate and subdominant balsam fir, would also tend to increase the production of staminate flowers, and in consequence, to increase the susceptibility of the balsam fir to budworm attack.

Large areas of upland forest in the Lake Nipigon and Black Sturgeon Lake area of Ontario have been characterized in recent years by decadent stands of 125 to 140-year-old trembling aspen, *Populus tremuloides* Michx. Within these stands, aspen trees 10 to 20 inches in diameter and 85 to 110 feet in height formed the major component of the tree cover, providing a dominant canopy that sheltered the large co-dominant white spruce, *Picea glauca* (Moench) Voss, and covered the smaller sub-dominant and intermediate white spruce and balsam fir. By 1950, when the present study was undertaken, these trembling aspen stands were almost completely disintegrated, both through death of standing trees and, more markedly, through windbreakage in mid-trunk. The characteristic appearance of these decadent, windbroken aspen stands is illustrated in Fig. 1. From this figure it can be readily appreciated to what extent these stands were originally dominated by mature trembling aspen, and to what extent the exposure of subdominant and intermediate balsam fir and spruce trees was increased by the break-up of this aspen canopy.

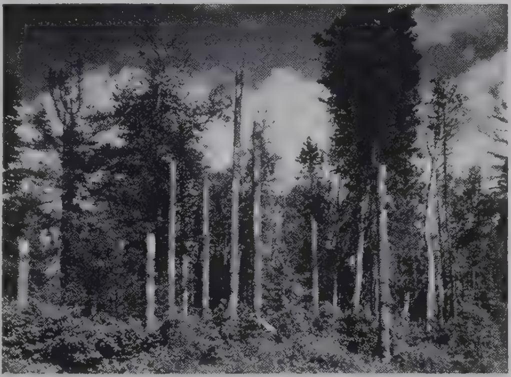

Fig. 1. Typical appearance of the decadent trembling aspen stands in the Lake Nipigon-Black Sturgeon Lake area of Ontario. Photograph taken near the Horan Creek study plot. Abundant shrub growth shown in this picture consists almost entirely of mountain maple, *Acer spicatum* Lam.

The principal objectives of this study may be summarized as follows: (1) to develop reliable techniques for determining the mortality history of the aspen overstory; (2) by means of these techniques, to determine the relation of aspen mortality to the forest tent caterpillar outbreak of the late 1930's; (3) to determine what influence the mortality and the defoliation of trembling aspen might have had on the exposure, flowering history, and consequent budworm susceptibility of the understory balsam fir trees.

METHODS OF STUDY

Statistical techniques developed for cross-dating the mortality of dead trees, and techniques for the collection and paraffin-impregnation of decayed wood from dead trembling aspen, have been presented in earlier papers (Ghent, 1952, 1954). Using these techniques it has been possible to establish with confidence the year of last growth of all the dead trembling aspen encountered during this study. Some of these trees had been dead for 25 to 35 years at the time the study material was collected, and from such trees the untreated wood could often be crumbled between the fingers to a fine dust. Fig. 2 illustrates the quality of ring differentiation obtained in freehand sections cut from paraffin impregnated fragments of two such trees.

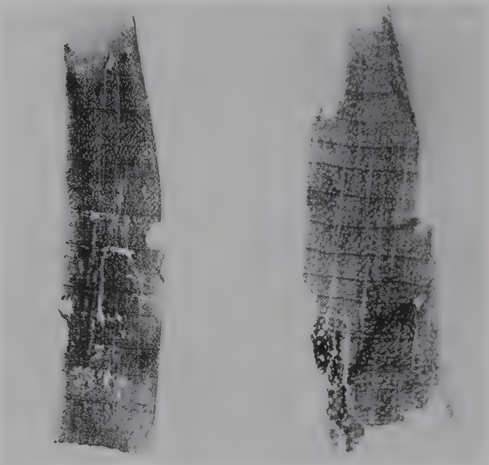

FIG. 2. Ring differentiation obtained in paraffin-impregnated fragments from dead trembling aspen trees. Sections prepared from trees that put on their last radial increment in (left) 1918, and (right) 1927. Study material collected in the field in the summer of 1953. Magnification x 10.

In order to relate overstory mortality in trembling aspen stands to the tent-caterpillar outbreak of the 1930 decade, it was desirable to establish the exact years of this outbreak in the Lake Nipigon-Black Sturgeon Lake area. It was necessary to rely mainly on the evidence of tree-ring suppression in living trembling aspen, but the interpretation of that evidence was facilitated by reference to accounts of the outbreak published at the time in the *Port Arthur News Chronicle*, and preserved in the files of that newspaper.

It was impossible to obtain information on the flowering history of balsam fir trees near the center of the Lake Nipigon budworm outbreak. At the center of the outbreak, near Gull Bay on the west shore of Lake Nipigon, the only balsam fir still living after the outbreak were scattered small trees previously suppressed by the stand that supported the budworm infestation. It was possible, however, to measure the flowering histories of two large balsam fir trees in a decadent stand of trembling aspen near Horan Creek, a small stream that flows into the west side of Black Sturgeon Lake about 40 miles south of the center of the outbreak. These trees, both about 10 inches in diameter, survived the spruce budworm infestation in sufficiently good condition to allow an accurate study of their flowering histories. Around these trees a circular plot approximately one-half acre in area was established. There were 36 dead trembling aspen within this plot, and study material was collected from these trees for cross-dating mortality. Since the flowering histories of the two large balsam fir appear to have been strongly influenced by the progress of break-up of the surrounding aspen overstory, and since the histories of break-up of the overstory at Horan Creek and at Gull Bay appear to have been almost identical, we may claim, by inference only, to have gained some knowledge of the probable flowering history of balsam fir at the center of the budworm infestation.

In the Gull Bay area, overstory mortality was measured on five circular one-tenth-acre plots, located systematically from a randomly established starting point. A total of 71 dead trembling aspen occurred on these five plots, and for each of these the year of last growth was also determined.

HISTORY OF THE FOREST TENT CATERPILLAR OUTBREAK

The first indication of the forest tent caterpillar outbreak that swept the Lake States and Ontario in the 1930 decade was a report in 1933 of severe defoliation in a small area below the Ontario border near Ely, Minnesota (Hodson, 1941). In 1934 the outbreak spread throughout northern Minnesota, and in this year the *Port Arthur News Chronicle* carried the first reports of defoliation in northwestern Ontario. Approximately 20 square miles of young birch and poplar were reported to be defoliated in the townships of South Gillies and Pearson, about 40 miles to the southwest of Fort William. By 1935 the forest tent caterpillar was reported to be causing severe defoliation around Fort William and Port Arthur, and for some distance to the west and southwest. There is no indication in the newspaper accounts that the Lake Nipigon-Black Sturgeon Lake area to the northeast of Port Arthur suffered severe defoliation at this time, and indeed the growth ring put on by trembling aspen in 1935 in this area was one of the largest rings that had been laid down since 1900. The forest tent caterpillar appears to have been active throughout northern Ontario in 1936, and during this season stories of disgruntled fishermen and campers turning back from caterpillar-infested woods near Port Arthur, Sudbury, North Bay, and other Ontario centers, became common in the *News Chronicle*. For the first time a few of these accounts specified areas immediately to the east and northeast of Port

Arthur, but it is evident from tree-ring analysis that no more than moderately heavy defoliation could have taken place in the Lake Nipigon-Black Sturgeon Lake area at that time. Whereas all aspen in this area show a substantial reduction in growth in comparison with the excellent growth of 1935, the 1936 growth ring was not so small as to suggest, by itself, a year of heavy defoliation.

During the next two years, 1937 and 1938, the *News Chronicle* continued to carry reports of province-wide defoliation, and it is for these years that two very minute rings were laid down by trembling aspen trees both at Black Sturgeon Lake and at Lake Nipigon. There is some evidence in the newspaper accounts that the outbreak was heavy to the northeast of Port Arthur for the first time during these years, for the first reports of severe defoliation are recorded from MacDiarmid, a small settlement on the east short of Lake Nipigon across from Gull Bay, and from other small centers in the Lake Nipigon area. Tree-ring analysis indicated marked recovery during 1939, and it is noteworthy that the only mention of the forest tent caterpillar in the 1939 newspaper files was an incidental observation that this insect was not in evidence that year. Taking together the evidence of growth-rings and newspaper accounts, there can be little question that 1937 and 1938 were the years in which defoliation of the aspen overstory in the Lake Nipigon-Black Sturgeon Lake area was sufficiently severe to have had a marked influence upon the exposure of understory balsam fir and spruce trees. Defoliation in 1936 may have slightly increased the exposure of these understory trees, but to a much lesser extent than what we may assume to have been the complete defoliation of the overstory during the two years that followed.

History of the Spruce Budworm Outbreak

Heavy defoliation of balsam fir trees in the Gull Bay-Chief Bay area of Lake Nipigon was first observed in 1943, but it was evident at that time that the outbreak had been in progress for some years (Belyea, 1952). Fettes (1950) was able to measure the defoliation of balsam fir trees as far back as the shoot growth of 1940, and found that in that year the spruce budworm population was sufficiently high to have removed just less than 90 percent of the needles. By careful examination of the leaf-scars, Fettes achieved some success at distinguishing between defoliation contemporaneous with the shoot growth and "back-feeding" of later populations on old foliage. In pushing back our knowledge of the budworm population to 1940 by this method, Fettes was still forced to leave his first measure of the population at an illogically high point for the initiation of an outbreak, and for this reason some attention was given to a technique (Ghent, in preparation) whereby a picture of the history of a budworm outbreak might be obtained from the evidence of damage to the leaders and primary laterals of balsam fir regeneration, caused by the feeding of late-instar larvae that dropped from the trees.

Data obtained with this technique are presented in histogram form in Fig. 3. Also shown in this figure, as a frequency polygon, are the measurements of defoliation obtained by Fettes (1950). It has been found characteristic of such comparisons between seedling damage and tree defoliation that the latter part of an outbreak is more accurately reflected than the earlier part, a discrepancy that can almost certainly be attributed to the greater availability of foliage on the trees during the earlier years of an outbreak. Bearing this in mind, it is apparent from Fig. 3 that the budworm population in 1939 had reached very nearly as high a level as that attained in 1940, the first year for which direct measurements of tree defoliation could be obtained. It is probably safe to infer that the high level of population indicated by the defoliation of 1940 had been attained in no more than two or three years of rapid growth from a relatively much lower level of population. Thus the beginning of the budworm population upsurge appears to have coincided almost exactly with the period of severe aspen defoliation by the forest tent caterpillar.

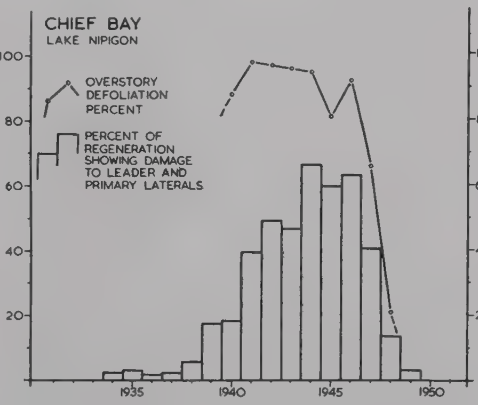

Fig. 3. A comparison of direct measurements of overstory defoliation (Fettes, 1950) with the per cent incidence of damage to leaders and primary laterals of balsam fir seedlings. Seedling data based on the inspection of 159 balsam fir seedlings collected near Chief Bay, Lake Nipigon.

Break-Up of the Aspen Overstory

The forest stands in the study areas at Horan Creek and at Gull Bay proved to be very similar in composition. In the Horan Creek area trembling aspen averaged 13.9 inches in diameter, and accounted for 62 percent of the total basal area of the stand. Balsam fir and white spruce averaged 8.2 and 6.4 inches in diameter respectively, and together made up 22 percent of the total basal area. A few individual trees of both species measured as much as 20 inches in diameter. The remaining 16 percent of the total basal area was made up of white birch, *Betula papyrifera* Marsh., balsam poplar, *P. balsamifera* L., and jack pine, *Pinus banksiana* Lamb. Trembling aspen in the Gull Bay forest were slightly larger, averaging 15.1 inches in diameter, and accounted for 79 percent of the total basal area. Balsam fir and white spruce averaged 5.9 and 10.1 inches in diameter respectively, and together made up 16 percent of the total basal area. The remaining 5 percent of the total basal area consisted entirely of white birch. The Gull Bay forest appears to have been a denser stand, there being 336 stems to the acre compared to 204 at Horan Creek. Both stands were on deep, fine sands, sufficiently fine in the case of the Horan Creek stand to suggest a wind-blown origin. Counts of growth rings on discs cut at stump height from living trees during the field seasons of 1952 and 1953 indicated that the aspen at Gull Bay all fell within the range of 125 to 130 years of age, while those at Horan Creek fell within the range of 135 to 140 years. This narrow range in the ages of aspen trees growing in dense stands is characteristic of the species, since aspen becomes established in dense stands by usurping an area as a pioneer species immediately after some ecologically catastrophic disturbance such as a severe fire or a clear-cutting. Since cutting operations in the Lake Nipigon-Black Sturgeon Lake area have been in progress for only a few decades, it is clear that these aspen stands can only be attributed to extensive fires in this area during the early part of the nineteenth century, and that logging practices played no part in developing what has proved to be a budworm-susceptible forest complex.

The progress of overstory mortality in these stands has been summarized in Fig. 4. Mortality data from the two sample areas are presented as cumulative frequency polygons plotted on a common percent scale. In both cases overstory break-up has tended to follow a sigmoid trend, and there is a striking similarity in the progress of mortality in the two areas. The earliest measured mortality at Gull Bay took place in 1918, and the incidence of additional mortality in 1919 and 1920 provides confirmation that the process of break-up began at that time. The cumulative mortality curve for Horan Creek rises more abruptly from an apparent beginning in 1924, but it is possible that a larger sample from this area might have included a few trees that had put on their last growth a few years earlier. By 1953, aspen mortality reached 98 percent at Gull Bay and 94 percent at Horan Creek. Sample size in both areas, dictated by the labor involved in determining the year of last growth of badly decayed material, places limitations upon the significance that may be attached to minor differences in the two curves, and the remarkable similarity in the history of break-up of the aspen canopies in the two areas remains the most striking feature of this figure.

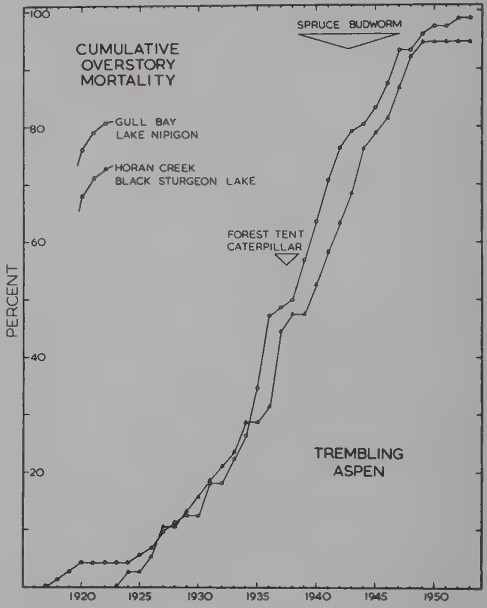

Fig. 4. Cumulative overstory mortality at Gull Bay, Lake Nipigon, and at Horan Creek, Black Sturgeon Lake. Horan Creek curve based on the cross-dated mortality of 36 trees; Gull Bay curve based on 71 trees.

A small triangle has been drawn to indicate the period of heavy forest tent caterpillar defoliation during 1937 and 1938. It is apparent that in both areas over 40 percent of the overstory had died before this time. Moreover, the only feature of these mortality curves that might possibly be associated with this period is the small "jog" in each at about the time of the forest tent caterpillar outbreak. Overstory mortality in these overmature aspen stands is largely attributable to trunk breakage during mid-summer windstorms when the crowns are in full leaf, a conclusion substantiated by direct observation in this area between 1949 and 1953, and by the appearance not only of the tops of the old stubs from earlier seasons, but of the outer growth rings of these trees as well. The unlignified outer ring of a trembling aspen that has been cut or windbroken in mid-summer takes on a bright orange or pinkish shade as it deteriorates, and the bright color of these outer rings could often be distinguished in study material collected from trees that had been dead for 15 or 20 years. Only a few of these trees showed evidence of a marked decline in the vigor of their ring growth before death, and it is noteworthy that calculations based on these ring measurements indicate that many of these tree maintained the same rate of basal area increment during the decade before windbreakage that they had maintained during the previous 80 years. In northern and northwestern Ontario, where trembling aspen regularly attain a breast-height diameter of 25 inches or more, it may then be the normal fate of the undisturbed trembling aspen to outgrow its structural limitations. In any event it is probable that the brief period of decreased mortality evident in Fig. 4 at the time of the forest tent caterpillar outbreak reflects the reduced wind resistance of the defoliated trees, and there would seem to be no other way in which the forest tent caterpillar outbreak can be said to have influenced the progress of break-up of these stands.

In the upper right-hand corner of Fig. 4 the period of spruce budworm defoliation has been indicated as beginning in 1939, the best approximation that can be made for the initiation of high population levels in the Gull Bay area. At Horan Creek, equally high population levels were not attained until about 1942. By the time the budworm outbreak began at Gull Bay, over 50 percent of the trembling aspen overstory had disintegrated both at Gull Bay and at Horan Creek. In patches throughout these stands, many of the balsam fir had been effecively open-growing trees for 10 to 20 years before the budworm outbreak, and as the mortality of overstory trembling aspen gradually increased to 30 and 40 percent, one may suppose that most of the balsam fir received full light for at least a portion of every day. In this picture of overstory mortality beginning as early as 1920, there is a history of progressively increased exposure far more likely to have influenced the susceptibility of the balsam fir to budworm devastation than any briefer history of exposure that might have waited upon the forest tent caterpillar outbreak for its initiation.

Balsam Fir Flowering History

In order to study the flowering history of balsam fir trees in relation to the mortality of the aspen overstory and in relation to the spruce budworm outbreak, it was necessary to adopt the inferential approach outlined in the section on methods of study. The necessity of so doing affords an excellent illustration of the devastation wrought by the spruce budworm in the Lake Nipigon forest area, since it was necessary, five years after the outbreak was over, to work in a stand 40 miles from the center of the infestation to find living balsam fir representative, in terms of size and exposure, of those trees that had supported the outbreak.

Two such trees were the 10-inch balsam fir around which the half-acre Horan Creek study plot was established. These trees were felled, and sample branches were taken at a series of six levels systematically distributed over the length of the crowns. On these branches each year's growth was sampled to the extent of 100 shoots, or sampled in its entirety if fewer than 100 shoots were available. The percentage of each year's shoots that bore remnants of the basal cups left by burst male flower buds was then determined. In this way percent flowering data were obtained for each year's shoot growth as far back as the late 1920's, and for one of the trees as far back as 1921. Small samples of shoot growth were available for nearly another decade on the branches from the lower levels in the crowns, and since no evidence of the persistent staminate flower cups could be found on these shoots, it is reasonable to conclude that an accurate picture of the initial years of flowering was obtained.

From the standpoint of the relative quantity of male flowers available to the spruce budworm, the more recent years of flower production, represented in the samples from all levels in the crown, must receive proportionately greater weight than the earlier years, represented only in the samples from the lowest levels. For this reason, the percent flowering data were totaled by years for the six levels, and the yearly totals divided in each instance by six, even though these totals might represent a contribution of data from only one or two levels in the case of an early year of flowering. In this way a hypothetical recent year in which 60 percent of the shoots bore male flowers at all six sample levels would appear in the final results as *60 percent flowering;* whereas an early year in which 60 percent of the shoots bore male flowers at only the lowest sample level in the crown would appear as *10 percent flowering.* It is appreciated that this averaging of percentage data is a departure from accepted arithmetic practice, but it seems that any alternative method, however much it might be more arithmetically refined, would need to give similar weight to the more recent years of flower production if it were to present a realistic quantitative expression of the availability of staminate flowers to the spruce budworm. The data, as treated, can no longer be considered *percentages* in a strict sense, however, and should be looked upon as *per cent indices.*

The results of this study have been summarized in Fig. 5. The tendency in balsam fir for years of peak flower production to be separated by one or two years of very low flower production is evident in this figure. The first evidence of flower production by either tree was found on the shoot growth of 1921 on tree "B," which was 50 years old at that time. Tree "A" showed no evidence of flower production until 1928, when it was 56 years old. Open-grown balsam fir in a stand a few miles from Horan Creek produced their first male flowers when they were only 27 years old, so that it may be safely concluded that trees "A" and "B" at Horan Creek had been prevented from flowering before the 1920 decade by the still-closed overstory canopy of trembling aspen.

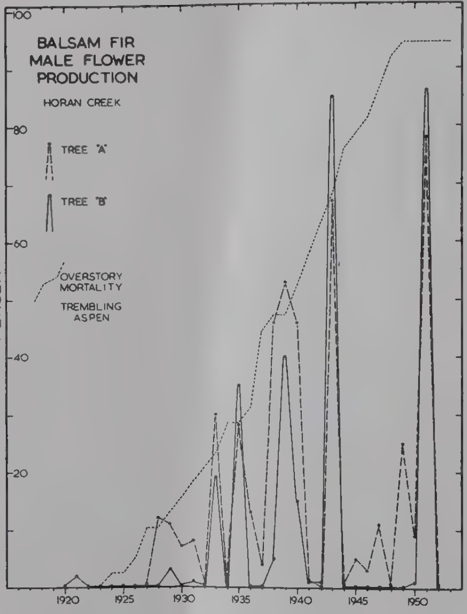

FIG. 5. A comparison of the histories of male flower production of two ten-inch balsam fir trees located approximately at the centre of the Horan Creek study plot, with the progress of overstory mortality repeated from Fig. 4 as a dotted line.

The progress of break-up of the trembling aspen canopy at Horan Creek, given originally in Fig. 4, has been repeated in Fig. 5 as a fine dotted line. The most striking feature of Fig. 5 is that the proportionate increase in the height of recurrent peaks in the flowering histories so neatly parallels the rate of increase in the overstory mortality. Even though the data presented represent only two trees, the hypothesis of a direct causal relation between overstory mortality and the intensity of balsam fir male flower production is clearly suggested.

ESTABLISHMENT OF A SHRUB LAYER

An interesting feature of the decadent trembling aspen stands at Horan Creek and at Gull Bay is the establishment of an almost unbroken shrub layer of vigorous mountain maple seedlings, *Acer spicatum* Lam. Equally interesting, though not at first so striking, is the almost total absence of trembling aspen sucker growth around the windbroken overstory trees. Such sucker growth does occur along the edges of roads passing through these stands, but within the stands themselves, with the exception of the occasional small opening in the mountain maple shrub layer, trembling aspen sucker growth is totally absent.

These observations suggested that it might be profitable to investigate the history of establishment of this mountain maple shrub layer, to see if it might not also be related to the progressive mortality of the aspen overstory. For this purpose a series of 1/160 acre plots (one-quarter chain square) was established in each study area. The mountain maple shrub layer was clear-cut on each plot, and the age of each stem determined by microscopic examination of the growth rings. Mountain maple stems show relatively little differentiation between early and late wood, and an unusually keen cutting edge must be employed to permit unobscured examination of the growth rings. Ring differentiation is improved if the stems are prepared for examination when still fresh and then allowed to become air-dry before examination. The early and late woods show some tendency towards a differential absorption of light-colored dyes, and an inexpensive orange ink was found to be of some assistance in bringing out the growth rings on some of the more obscure basal sections.

A clear-cutting of eight plots established at Horan Creek yielded a collection of 733 basal sections; in the same way five plots at Gull Bay yielded 341 basal sections. These collections indicate that there were approximately 14,000 mountain maple stems per acre in the Horan Creek area and approximately 11,000 per acre at Gull Bay. Although no real precision can be claimed for these estimates, the indicated density of one mountain maple stem to every 3 to 3½ square feet of ground is entirely in keeping with the impression gained of an unbroken layer of mountain maple seedlings, each of which tends to develop, as space permits, into a bushy shrub between 8 and 10 feet in height.

The cumulative establishment of mountain maple seedlings, as determined from age data gathered in this study, has been summarized for the two areas in Fig. 6. Curves of overstory mortality, originally given in Fig. 4, have been repeated in Fig. 6 as fine dotted lines. Minor differences in the shape of the two curves are evident. Mountain maple establishment at Horan Creek appears to have been sensitive to the early years of overstory mortality, and to have taken a second spurt in the mid 1940's, possibly associated with the additional thinning of the overstory caused by the defoliation of spruce and balsam fir by the spruce budworm. At Gull Bay, establishment of mountain maple seedlings proceeded slowly until 1937 or 1938 and then accelerated markedly. This acceleration may have been initiated by the increased exposure of the forest floor associated with overstory defoliation by the tent caterpillar. Disregarding such minor differences, it is evident that in both study areas there has been a strong correlation between the progress of break-up of the overstory and the progress of establishment of the mountain maple shrub layer.

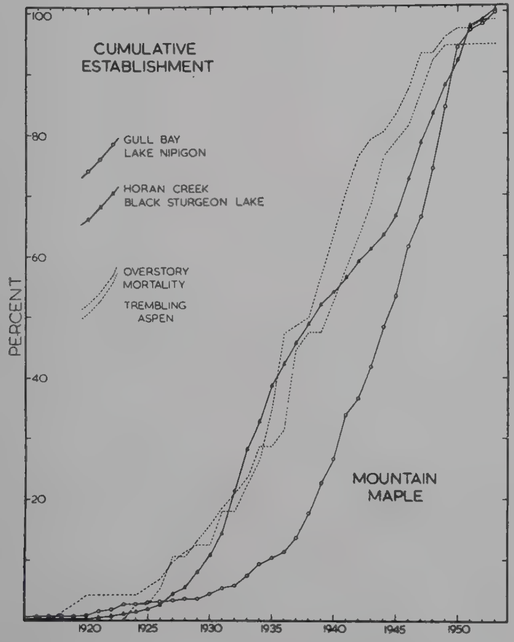

Fig. 6. Cumulative establishment of mountain maple seedlings at Horan Creek and at Gull Bay compared to the histories of overstory mortality repeated from Fig. 4 as fine dotted lines.

In this correlation we have the probable explanation for the absence of trembling aspen sucker growth already noted. The well-known ability of trembling aspen to regenerate by sucker growth following a clear-cutting evidently did not operate under the conditions of partial shade engendered by the gradual break-up of the overstory. Rather, it would seem that the small openings brought about by the tree-by-tree removal of the overstory over a 30-year period were occupied more or less as they were produced by mountain maple seedlings, evidently better suited to such conditions of partial shade. In this connection the establishment in the same forest areas of extensive mountain maple shrub layers following budworm devastation of pure coniferous stands is also noteworthy. Similar age-studies indicate that although the nucleus of a shrub layer was present for many years in the form of scattered mountain maple shrubs, the shrub layer as such did not become established until the period of severe defoliation and progressive mortality of the coniferous overstory.

Discussion

The Lake Nipigon spruce budworm outbreak began in an area characterized by decadent aspen stands, the remnants of which had been severely defoliated by the forest tent caterpillar just before the spruce budworm population reached outbreak proportions. Wellington *et al.* (1950) suggested that in such instances as this the forest tent caterpillar might be a direct ally of the spruce budworm by increasing the exposure of understory spruce and balsam fir trees, thereby extending the area of forest conditions suitable to the budworm and in this way increasing the severity of the budworm outbreak. It was also suggested that although 20 years might be required to eliminate an original stand of decadent, overmature poplar, severe defoliation of such trees by the tent caterpillar might shorten the period of elimination of the decadent stand to as few as five to seven years. It was postulated that this accelerated decadence, if it occurred during the climatic fluctuation in advance of the one associated with the spruce budworm, would greatly increase the susceptibility of the area to outbreaks of this insect by hastening the succession of the coniferous component of the stand.

The inference that the rate of elimination of these stands would be appreciably accelerated by forest caterpillar defoliation receives no support from the data collected in this study. Both at Horan Creek and at Gull Bay the break-up of the trembling aspen overstory began at least 15 years before the forest tent caterpillar outbreak, and had reached a rate during the years immediately before the outbreak fully as rapid as that displayed thereafter. From the data given in Fig. 4 the only possible effect in terms of tree mortality that might be attributed to defoliation is a reduction in the incidence of windbreakage during the period of heaviest defoliation.

It is apparent that the succession of the coniferous component of these stands was being promoted for a period of 20 years before the spruce budworm population reached outbreak proportions. Not only is this the logical consequence of the indicated history of overstory mortality, but it is also directly supported by what evidence it was possible to gather on the flowering history of the balsam fir. It is entirely questionable whether conifer succession would have been sufficiently advanced to support a budworm outbreak in these stands if the process had not started long before the forest tent caterpillar infestation of 1937-1938.

Wellington *et al.* laid their greatest stress upon the least elaborate of the possible influences that the forest tent caterpillar might have upon the spruce budworm: that the defoliation of aspen canopies might provide the spruce budworm with more extensive areas of suitable forest conditions, thereby permitting the budworm to become established in stands where it might otherwise be excluded. There is no evidence in the present study to contradict this suggestion as a possible generality. In the particular set of conditions that existed at the center of the Lake Nipigon outbreak, however, there is no necessity to call upon this possible factor to account for the devastation wrought by the spruce budworm. While it might be argued that the devastation of the balsam fir component of these decadent aspen stands might have been delayed without the intervention of the forest tent caterpillar, it is noteworthy that the budworm population persisted at a high level in the Lake Nipigon area until 1946 and declined in subsequent years only after it had exhausted its food supply. By 1946 windbreakage had accounted for 80 percent of the aspen overstory, and the fragments of canopy provided by the few surviving trees afforded no protection from the spruce budworm. Even if one goes back to the beginning of the budworm outbreak, the deterioration of these overmature aspen stands had already advanced to such an extent that there would seem to be no reason to suppose that the spruce budworm would have been excluded from these stands if the outbreak of the forest tent caterpillar had never occurred.

The present study demonstrates that in the chronology of these outbreaks the defoliation of the remnants of the aspen canopy by the forest tent caterpillar and the upsurge of the budworm population coincided exactly. The high populations of spruce budworm evidently present in 1939 must have been the product of some improvement in the survival or fecundity of the budworm population of 1938, and the 1938 population, in turn, in all probability represented a substantial increase over the population of 1937. The inescapable suggestion prompted by this exact coincidence is that the forest tent caterpillar effectively "triggered" the explosive increase in the budworm population by creating conditions that provided the spruce budworm with the extra vigor required to reach outbreak proportions. Since there were areas of relatively pure balsam fir and spruce unshaded by aspen overstories near the center of the Lake Nipigon outbreak, this possible "triggering" effect of overstory defoliation would again seem to be an unnecessary factor to account for the outbreak. At the same time, the area of the initial infestation in the Lake Nipigon outbreak was small in comparison with the area of forest that sustained the outbreak when it had gained momentum; it is possible that the sudden and complete exposure of balsam fir and spruce trees that had been becoming progressively more exposed for 15 to 20 years produced in a small area conditions more favorable to the spruce budworm than those existing in pure coniferous stands nearby. As our knowledge of the ecology of the spruce budworm is extended, it is increasingly evident that the forest conditions necessary for the growth of a population to outbreak proportions are very different, and certainly much more critical, than those which permit the maintenance of an outbreak that is once established.

It is likely that the aspen component of future stands in the Lake Nipigon and Black Sturgeon Lake areas will be much reduced, for, at present, aspen sucker growth is limited to scattered openings in the mountain maple shrub layer. Most of the advanced regeneration of spruce and balsam fir is surviving beneath this shrub layer, although it is not uncommon to find small pockets in which balsam fir and spruce seedlings have been choked out by the vigorously competitive mountain maple. However, the survival of the more advanced coniferous regeneration, much of which is now working its way through the mountain maple shrub layer, appears to be assured. Thus, with the exception of trembling aspen, it is probable that the next stage in forest succession will be a stand similar to that which was destroyed: a climax stand of spruce and balsam fir liable to devastation by the spruce budworm during some period towards the end of the present century.

SUMMARY

(1) This study was undertaken to determine the relation of aspen mortality in the Lake Nipigon forest area of Ontario to the forest tent caterpillar outbreak of the late 1930's, and to determine what influence aspen mortality might have had on the exposure, flowering, and consequent budworm susceptibility of understory balsam fir and spruce trees later devastated by the spruce budworm.

(2) Evidence of growth-ring suppression in living trembling aspen trees indicates that aspen in this area were moderately defoliated in 1936 and heavily defoliated in 1937 and 1938. This interpretation was substantiated by accounts of the forest tent caterpillar outbreak found in contemporary issues of the *Port Arthur News Chronicle*.

(3) Evidence of damaged leaders and primary laterals of balsam fir seedlings, caused by late-instar spruce budworm larvae dropping from the overstory trees, indicates that the spruce budworm population built up rapidly during the two or three years before the earliest measured overstory defoliation in 1940. This places the probable initiation of the budworm population upsurge at a time that appears to coincide exactly with the period of heavy aspen defoliation by the forest tent caterpillar.

(4) At Gull Bay, on the west shore of Lake Nipigon near the center of the spruce budworm outbreak, aspen mortality began as early as 1918; and at Horan Creek, 40 miles to the south near Black Sturgeon Lake, as early as 1924. Aspen mortality appeared to be almost entirely attributable to windbreakage of the aspen trunks. Over 40 percent of the overstory had disintegrated in this way before heavy defoliation by the forest tent caterpillar occurred, and over 50 percent had died before the spruce budworm reached outbreak proportions.

(5) Flowering histories of two 10-inch balsam fir trees in the Horan Creek study plot indicated that the initiation of staminate flower production had coincided with the initiation of aspen overstory mortality, and that the progressive increase in flowering abundance had paralleled the progress of aspen mortality.

(6) Establishment of mountain maple shrub growth was also found to have closely paralleled the progress of aspen mortality, a factor to which the absence of trembling aspen sucker-growth reproduction in these stands may probably be attributed.

(7) The suggestion of Wellington *et al.* (1950) that the progress of overstory elimination was accelerated by forest tent caterpillar defoliation, and that the succession of the coniferous component of these stands was hastened in this way, receives no support from this study.

(8) While the present study does not contradict the suggestion that forest tent caterpillar defoliation may have extended the area of balsam fir and spruce forests susceptible to the spruce budworm, such a postulate now seems to be unnecessary to account for the devastation of these mixed aspen-balsam fir stands during the Lake Nipigon spruce budworm infestation.

ACKNOWLEDGMENTS

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SOME OBSERVATIONS ON SNAKE ACTIVITIES AND POPULATIONS

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In recent years much emphasis has been placed on animal activity and population studies. This has been particularly true for game species, and those forms showing marked population fluctuations. It is apparent from the literature that little information is available for poikilothermic vertebrates with the exception of fishes. In a detailed review of vertebrate populations, Errington (1946) found little to report on reptiles. Data, largely on snake activity, are limited principally to studies by Klauber (1924), Brimley (1925), Loveridge (1927), Conant (1938), Seibert and Hagen (1947), and Seibert (1950 and 1951). These investigations yield information on population density and seasonal occurrence of snakes but virtually no year to year population levels are revealed. Gloyd (1944) suggests that populations of snakes do vary from year to year although no regular peaks of abundance have been recorded. From data reported for Panamanian areas (Dunn 1949) it seems apparent that there are fluctuating population levels.

An opportunity to begin a study of seasonal activity and number of snakes resulted from a three-year investigation of the bob-white quail, *Colinus virginianus*, in southeastern Iowa (Klimstra 1950a). During this time 16 species of snakes were recorded (Klimstra 1950b). These observations were conducted on the Eldon Research Area, a 1600 acre tract located in sections 4, 5, 8, and 9, Salt Creek Township, Davis County. In topography the area was largely upland with about one-fourth a bottomland adjacent to a large creek. Two-fifths of the upland supported open to dense stands of third-growth oak-hickory, *Quercus-Carya*, which in recent years had been repeatedly burned and intensely grazed. The remainder was in permanent pastures and small, irregular, cultivated and idle fields. Erosion was severe, pastures were overgrazed and weedy, and encroachment of woodlands was evidenced by numerous shrubs in most fields. Lowland areas were intensively cultivated, the fields being small, irregular, and bordered by mature stands of trees and shrubs.

From 1946 through 1948 these observations were conducted in Iowa and from 1950 to date they have been restricted to southern Illinois. The Iowa studies were considerably more detailed than those made in Illinois where only general population levels have been evaluated from various field investigations in progress. In Iowa continuous observations were made while living on the research area during March 26 to September 15 in 1946 and during March 26 to September 4 in 1947 and 1948, respectively. Except during inclement weather, field studies were conducted daily during this period. When not in residence, two to four trips per month were made to the area and a minimum of two full days were spent in the field. Actual man hours in the field were comparable for each month of the three years.

Because field work during April to September (1946-1948) was concerned with finding quail nests, almost every acre of land which might conceivably provide nesting sites was thoroughly searched three to five times each season. The nest hunting was accomplished systematically by working the areas in parallel strips six to eight feet wide and examining the ground cover with the aid of a walking stick. As a result of this method it was believed that a large proportion of the snakes in the open were observed. In addition, small grain and hay harvesting machines were followed when in operation. Numbers of snakes recorded were based on frequency of occurrence resulting from these daily observations. All specimens observed during any one day in the field

Table I. Three year summary of frequency of occurrence of snakes on Eldon Research Area, Davis County, Iowa, 1946-48

	Jan.			Feb.			Mar.			April			May			June			July			Aug.			Sept.			Oct.			Nov.			Dec.			Total	%
Species	46	47	48	46	47	48	46	47	48	46	47	48	46	47	48	46	47	48	46	47	48	46	47	48	46	47	48	46	47	48	46	47	48	46	47	48		Total
Coluber constrictor flaviventris	0	0	0	0	0	0	2	0	0	7	2	1	90	71	35	71	40	20	36	20	7	10	7	2	11	8	2	28	1	0	4	0	0	0	0	0	475	55.88
Elaphe o. obsoleta	0	0	0	0	0	0	0	0	0	4	0	1	60	22	10	40	19	7	9	7	6	4	4	2	9	3	3	21	0	0	2	0	0	0	0	0	233	27.42
Heterodon c. contortrix	0	0	0	0	0	0	0	0	0	4	0	0	18	12	6	10	5	2	3	1	1	1	0	0	4	1	1	8	1	0	0	0	0	0	0	0	78	9.18
Natrix s. sipedon	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	9	6	2	7	0	2	0	1	1	4	2	1	11	0	0	1	0	0	0	0	0	50	5.88
Thamnophis sirtalis parietalis	0	0	0	0	0	0	1	0	0	0	0	6	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	4	0	0	0	0	0	0	0	0	14	1.64
Total	0	0	0	0	0	0	3	0	0	15	2	8	169	106	54	130	70	31	55	28	16	15	12	5	28	15	7	72	2	0	7	0	0	0	0	0	850	100.0
3 yr. total per month	0			0			3			25			329			231			99			32			50			74			7			0			850	
% total per mo. for 3 yrs.	0			0			.35			2.94			38.71			27.18			11.65			3.77			5.88			8.71			.81			0			100.0	

were recorded as to species, time, and location. It was believed that little if any duplication of snakes occurred in any one day's count.

The climatic conditions during the Iowa investigations were variable and somewhat abnormal (Klimstra 1950a). Record-breaking rainfall occurred during June of 1946 and 1947 and resulted in floods which covered a large portion of the lowlands on two occasions each year. Drought followed these heavy rains of both years and was especially severe in 1947 when virtually no rainfall was recorded during July, August, and the first two weeks of September. For 1946 temperatures considerably above average were recorded from January through April, and October through December while during the summer months, May to September, they were markedly below the norm. In 1947 temperatures were below the normal through most of July, but above the average during August to October. The 1948 temperatures and precipitation were more nearly normal than the two previous years.

Seasonal Activities

During the three years in Iowa 850 observations of the five most abundant species on the Eldon Research Area were recorded (Table I). Blue racer, *Coluber constrictor flaviventris,* yielded approximately 56 percent; pilot black snake, *Elaphe o. obsoleta,* 27 percent; hog-nosed snake, *Heterodon c. contortrix,* 8 percent; common water snake, *Natrix s. sipedon,* 6 percent; and red-barred garter snake, *Thamnophis sirtalis parietalis,* 2 percent.

For each species two peaks in seasonal abundance were in evidence (Fig. 1), a situation similar to that recorded by Conant (1938) for snakes in Lucas County, Ohio. Initial snake activity in the spring was recorded in late March when *Coluber* and *Thamnophis* appeared. *Coluber, Elaphe,* and *Heterodon* showed a spring climax during May while *Thamnophis* and *Natrix* were most abundant during April and June, respectively. These periods of abundance were followed by sharp declines with the most infrequent observations recorded in August. The low in August was followed by a gradual increase through September to a fall peak of abundance in October which was followed by a nearly complete absence of snakes by November (Fig. 1). When evaluated on a yearly basis the same general seasonal distribution was apparent for each species except possibly *Thamnophis,* which was represented by too few specimens to be considered significant (Table I). Similar seasonal occurrences of snakes have been reported by other investigators including Loveridge (1927), Klauber (1924), Brimley (1925), and Fitch (1949).

Conant (1938) found that the greatest number of snakes was seen in April. Because of the large number of *Thamnophis* (51.4 percent of all collected) recorded by Conant, the April peak as compared to that of May in Iowa is not surprising. *Coluber, Elaphe,* and *Heterodon* showed the same peak in May in both Ohio and Iowa. *Natrix sipedon* was observed in Iowa to be most active a month later than Conant reported (Fig. 1). In fall, the peak in activity for all species was reached in October in both midwest areas. However, in Ohio this was reflected largely by the numbers of *Storeria* and *Thamnophis.*

Several factors might be considered which in some way affect activity of snakes and in turn regulate the frequency with which individuals are observed. As with many animals, snakes respond to the reproductive urge in the spring by seeking out mates, resulting in greater movement, especially as they emerge from hibernating sites. Klauber (1924) believed this to be an important factor in activity. Generally, egg-laying and giving birth might be expected to result in decreased

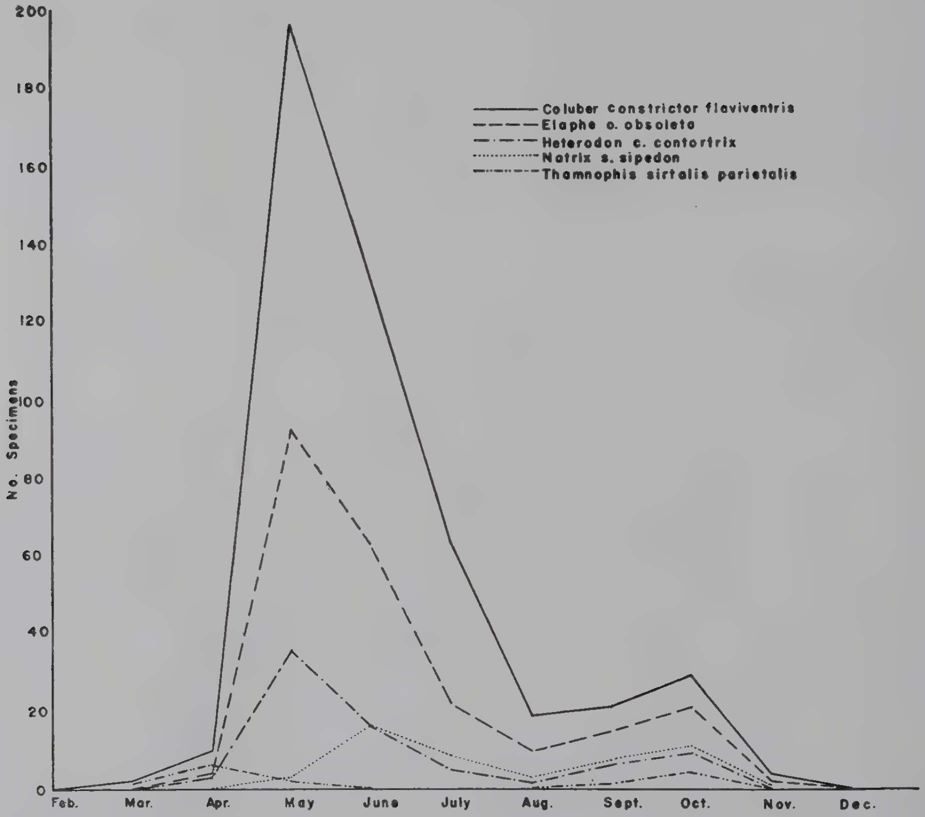

FIG. 1. Comparison of total populations and seasonal abundance of five snakes, 1946-1948, Eldon Research Area, Davis County, Iowa.

activity for females. Fitch (1949) observed that among rattlesnakes the adult female was almost completely absent during hot summer months, the period when most snakes produce young. As the young are difficult to observe, their presence does not necessarily increase the number of observations.

Food requirements could also be a factor influencing activity. Greater urge and need probably occurs in the spring due to reproduction and resulting increased metabolism as well as a need following depletion during hibernation. It has been observed that some snakes are nearly or entirely nocturnal in feeding (Klauber 1924). With certain forms this behavior is more or less normal during the entire non-hibernating season whereas others assume this behavior only during the hot summer months. For further consideration is the fact that a scarcity of food might encourage greater activity because of the necessity to search more intensively for food. Perhaps the small spurt in activity in the fall results from preparation for hibernation by increased feeding activity and movement to den sites.

Brimley (1925) has suggested that sight records of snakes might be closely related to vegetational development as dense cover would hinder field observations. Quite logically this might occur because of the progression of vegetation from very little in the spring to heavy growths by fall. However, because of the nature of the Iowa studies, the opportunity to find specimens was not believed to be affected markedly.

Although the above factors are believed to play some role, the degree being questionable, it is thought that climatic conditions affect more importantly the occurrence or lack of occurrence of snakes at any given time of the year. Whereas the restrictive aspects of low temperatures on cold-blooded forms are understood, the detailed effects of high temperatures are not. Loveridge (1927) considered the heat of June an important factor

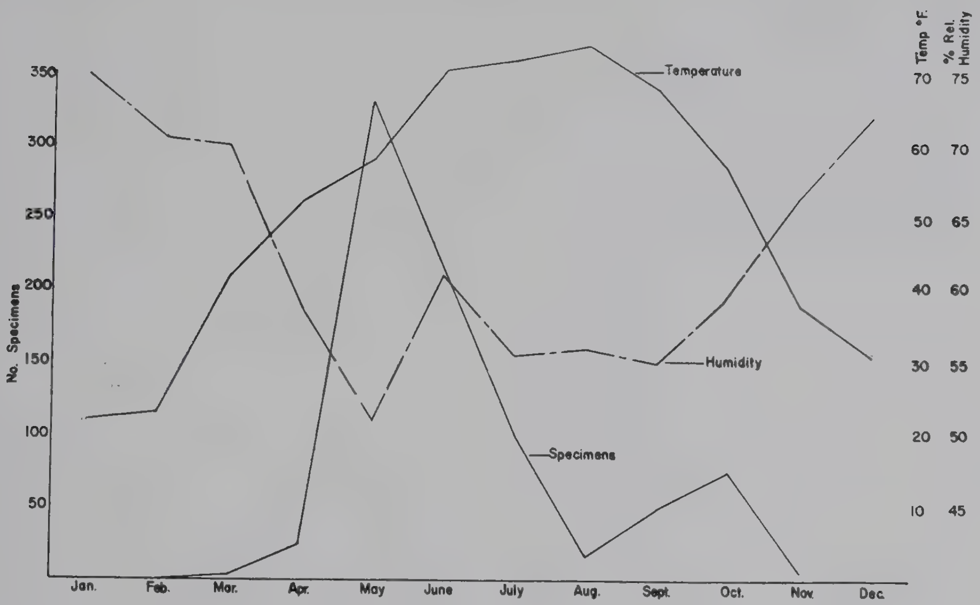

FIG. 2. The seasonal occurrence of a snake population correlated with mean monthly temperature and relative humidity, 1946-1948, Eldon Research Area, Davis County, Iowa.

in snake activity and believed that the daily high should fall between 80-96°F and not below 76°F. Seibert and Hagen suggested that optimum adjustment occurred between 50-86° and snakes retreated underground beyond these limits. It has been noted that below-normal temperatures in spring delay emergence from hibernation as much as 5 weeks (Fitch 1949). Lueth (1941) found that caged specimens were much more susceptible to disease after a period of cold weather and reported a correlation between air temperature and aggressiveness.

In correlating the seasonal activity of snakes with temperature, peaks in snakes observed occurred when mean temperatures were approximately 58°F both in the spring and fall seasons (Fig. 2). These represent an 8° higher mean temperature than that reported as the critical point in Ohio (Conant 1938). Minimum seasonal activity correlated with both low and high mean temperatures. The mean temperature in August (78°) correlated with the low mid-summer snake population whereas activity in the spring began when mean temperatures approached 40° and declined in the fall at a similar mean temperature. The latter was likewise observed by Seibert and Hagen (1947).

A relationship between relative humidity and snake activity was not readily apparent (Fig. 2). As activity increased in the spring, humidity decreased, a condition also evident in late summer. However, in early fall both activity and humidity increased until mean temperatures approached 40° at which time the activity declined sharply. Humidity during the period of observations did not closely approach the normal pattern during May and June either when considered on an individual year basis or when the three years were combined. With a minimum amount of interpolating it might be observed that greatest activity seemed to be associated with a humidity between 56 and 60 percent along with a mean temperature of 58° in both spring and fall (Fig. 2). Any interpretation of the effects of humidity, however, is admittedly weak.

Total precipitation seemed to show no correlation with seasonal occurrences of snakes. Here again extremes in both minimum and maximum rainfall were experienced during the three years of the Iowa studies. Conant (1938) was of the opinion that declining precipitaiton might in some cases result in more difficulty in finding snakes because they retire into inaccessible places, but in other cases make it more easy because of their being concentrated in limited sites.

SUGGESTED POPULATION LEVELS

Whereas the previous sections illustrate the relative degree of seasonal activity of snakes as suggested by the number of observations within a given year, this section is an attempt to evaluate the change in numbers of snakes from year to

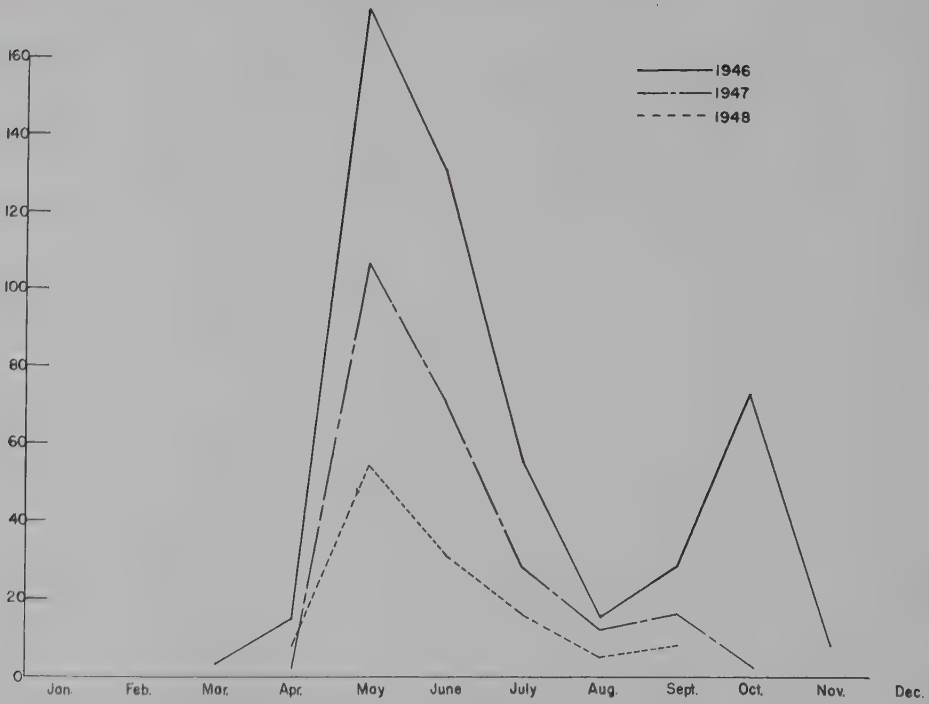

FIG. 3. Seasonal and yearly abundance of snake populations, 1946-1948, Eldon Research Area, Davis County, Iowa.

year. That snake populations do fluctuate from year to year has been documented. Gloyd (1944) suggested that such things as variations in food supply, enemies, and disease might be important factors in snake population fluctuations and that such factors in themselves might possibly be cyclic in nature. Data for Panamanian snakes (Dunn 1949) showed marked yearly differences in snake numbers that were deposited in various collections. Observations by Seibert (1950, 1951) and Fitch (1949) indicated that striking yearly variations in numbers were not uncommon.

Activity levels recorded in southeastern Iowa for 1946, 1947, and 1948 showed not only yearly variations in numbers but a 76 percent decline in specimens observed from 1946 to 1948 (Fig. 3). This represented a 53 percent and 52 percent reduction from 1946 to 1947 and from 1947 to 1948, respectively.

In an effort to account for the population decline experienced on the Iowa area, several factors including food, enemies, disease and intra-specific competition were considered. However, time did not permit a well planned attack for pursuit of all plausible conditions which may have led to a reduced population.

According to Fitch (1949) food must ultimately limit snake populations but just how this is accomplished is not clear. He has suggested, however, that there are many kinds of prey species available and, with snakes having a relatively wide range of food, a reliable and constant food supply would be prevalent in most environments even during periodic shortages of individual food items. Rather than a direct factor, food shortages possibly result in indirect adversities as losses may be heavy during hibernation as the result of snakes being in poor physical condition from a lack of foods prior to hibernating. Such shortages can also affect reproduciton through the physical condition of the parents which could possibly result in insufficient stored food in the eggs for developing young. Because young are less adept in capturing prey, lack of food might be most effective in reducing this age-class in a given snake population.

A limited amount of data was available on populations of certain potential snake foods. Observations of small mammal numbers were made from trapping, field sign and occurrence in diets of red foxes, *Vulpes regalis,* and great horned owls, *Bubo virginianus* (Scott and Klimstra 1955).

Trapping results showed a general decline in all forms of *Peromyscus* and *Microtus* represented on the research area. Occurrences of *Synaptomys, Reithrodontomys, Cryptotis, Blarina,* and *Scalopus* in fox fecal passages suggested declining populations during this study. At this same time the cottontail rabbit, *Sylvilagus floridanus,* population was also passing through a cyclic "low." Such declines as here experienced were synchronized with similar population levels throughout the midwest (Scott and Klimstra 1955).

Although no specific efforts were made to evaluate insect numbers, there was no apparent shortage or change in numbers except in 1946. Appearing in phenomenal numbers was the periodic cicada, *Magicicada* spp., which reached its peak during June. The orders Orthoptera and Coleoptera, which made up about 70 to 90 percent of the annual insect occurrence in the diet of the red fox (Scott and Klimstra 1955), remained relatively constant, at least in the foxes' diets.

Except for the bob-white quail, no data on avian population levels were considered applicable to these observations. Data on nesting robins (unpublished) showed fewer robin nests in 1948 than in 1946. However, these observations were not considered sufficiently extensive to warrant a judgment on comparative population levels. Bobwhites showed a definite decline from 1946 to 1948; the fall of the later year showed a slight increase, however.

Although no counts were made, Amphibians seemingly increased in number and became more widely distributed on the research area because of new impoundments. In addition to several existing permanent and semi-permanent streams and ponds, three permanent ponds were constructed in 1946. Thus, despite drouth conditions, there was not a general loss of suitable habitat during the course of the study.

Admittedly, predation as a limiting factor in this study is difficult to evaluate, but from limited data it seems unlikely that this was an important factor in the population decline. The populations and feeding habits of two principal predators on the research area were carefully recorded. It was of interest to note that both the red fox and great horned owl populations declined markedly during the three-year period (Scott and Klimstra 1955). Resident populations of red foxes, were as follows: 1946, 6 adults and 11 young; 1947, 8 adults and 11 young; and, 1948, 2 adults and 4 young. For the respective years the great horned owl showed 2 adults, 6 adults and 3 young, and no adults. Other known snake predators were considered scarce.

Snake remains occurred 14 times in 1450 fox scats and 2 times in 126 caches and trail items during 1946-1948. In 98 pellets gathered from three tethered young great horned owls in 1947 (only year pellets available) snakes occurred 18 times. No snake remains were found in pellets gathered at three owl nests in 1947. These data suggest that the owls make greater utilization of snakes than foxes but in neither case were snakes an important ranking food in the respective diets. It was of interest to note that the frequency of occurrence of snake remains in the foxes' diet did not reflect the declining snake population. The red-barred garter snake, although the least abundant of the five forms considered in this study, yielded percentage-wise the largest segment of its numbers to these two predators. Possibly the habits and environment utilized by this species made it more susceptible. Generally, the owls utilized the blue racer somewhat in proportion to its abundance. Because food habits of snakes were not investigated no evaluation can be made of inter- or intraspecific utilization.

Disease as a limiting factor was not observed but this would be almost impossible to evaluate in a wild population. Climatic conditions which favored extensive losses conceivably existed in 1946 during May to September and in 1947 during January to July as temperatures were markedly below normal. Lueth (1941) reported heavy mortality in collections 2 weeks following sharp drops in temperatures. It was not believed, however, that temperatures during the current study were sufficiently critical to have become effective in this respect.

Although inter- and intra-specific compeition is an important regulator as far as numbers of some species are concerned, no evidence can be offered with regard to the unusually high 1946 snake population. The greatest density observed was in June of 1946 when 16 blue racers and 6 pilot blacks were found in a 0.4 acre grassy plot. This did not approach the number of *Thamnophis* reported by Seibert (1950 and 1951) which apparently showed no adverse results.

As a result of continued field observations following transfer of residence from Iowa to Illinois, a total of 9 years of population levels of snakes in the midwest are available (no data for 1949). Indicated in Figure 4 are the specimens observed per man hour in the field for 1946-1948 (southeast Iowa) and for 1950-1955 (southern Illinois). Peaks are evident for 1946 in Iowa and 1952 in Illinois with lows occurring in 1948 (Iowa) and 1954 (Illinois). Unfortunately, no data are available prior to 1946 and for 1949. According to

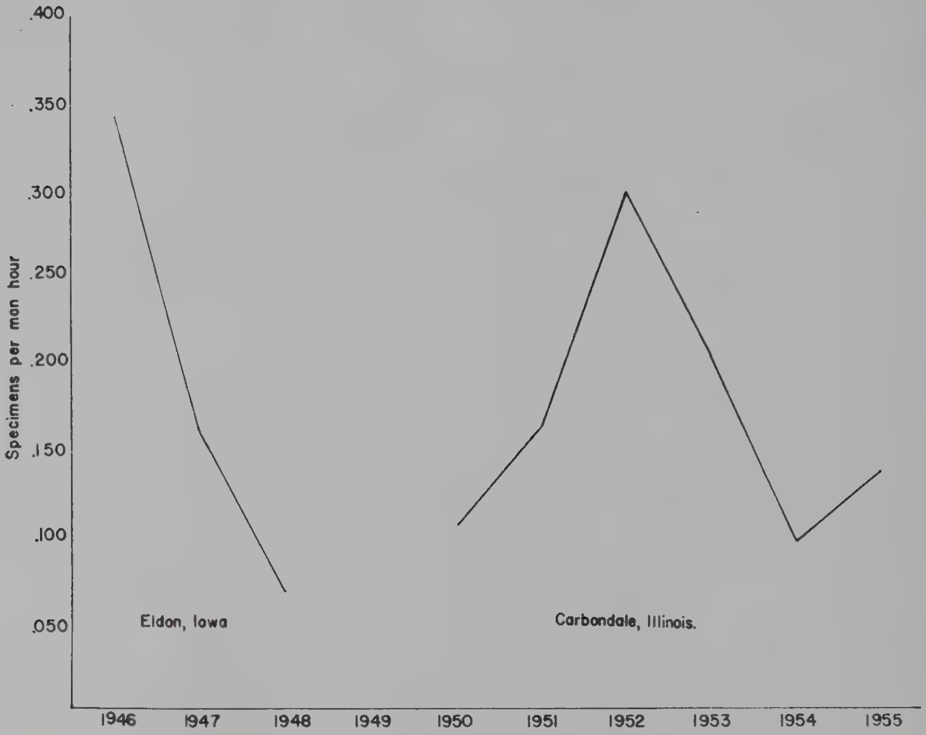

FIG. 4. Number of all snakes observed per man hour in the field, 1946-1955.

information provided by several southern Illinois collectors, 1945 was an unusually good year to obtain specimens. A not too authentic report from Iowa suggests that 1952 showed a high population level in Iowa. These data indicate that possibly snakes do fluctuate in numbers and that the fluctuations appear to be synchronized over an extensive area. It must be pointed out, however, that a more careful evaluation of climatic effects on snake activity is necessary. It is entirely possible that under some yearly conditions, even though snakes may occur in good numbers, the opportunity for observations in the field may be reduced significantly.

An analysis of the climatic conditions represented when both the Iowa and Illinois populations began the decline from so-called peaks in number is a point of interest. Both the summers of 1946 and 1952 were the beginning of drouth conditions. The first extended, however, for only two successive years whereas the later extended from 1952 through 1954. The build-up period in Illinois (1950 through 1951) to a peak in 1952 was characterized by unusually heavy spring and early summer rainfall. The increased number recorded for 1955, however, was not correlated with similar conditions as rainfall in Illinois did not approach the average.

SUMMARY

Observations of seasonal activities and numbers of snakes were conducted in Iowa, 1946-1948, and limited studies were continued in Illinois, 1950-1955. Iowa data for five species of snakes indicated two peaks, May and October, in seasonal abundance for each species. Possible factors responsible for seasonal increase and decrease in snake activity are discussed. Climatic conditions, especially temperature, seemed to be correlated closely with activity. Greatest activity was associated with mean temperatures of 58°F, and least activity with around mean temperatures of 40° and 78°. Data are presented which suggest that snake populations fluctuate.

Acknowledgments

This paper represents a contribution from Project No. 42, Cooperative Wildlife Research Laboratory, Southern Illinois University. Iowa data were accumulated while a research associate and fellow with the Iowa Cooperative Wildlife Research Unit. Encouragement during the initial phases of this study and criticisms in preparing the manuscript by Dr. Thomas G. Scott, Illinois Natural History Survey, are gratefully acknowledged. Dr. Hobart Smith, University of Illinois, was most helpful in suggesting literature sources and methods of evaluating the data. Several staff members of the Research Laboratory contributed by recording snake observations during various field investigations.

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ALTERATION OF MICROCLIMATE IMPOSED BY POPULATIONS OF FLOUR BEETLES[1] (*TRIBOLIUM*)

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That heat, moisture, and light are important factors in the survival of animals is substantially documented in ecological literature (Allee, *et al.*, 1949; Clarke, 1954; Andrewartha and Birch, 1955). To date the importance of these invironmental factors has been measured primarily by macroclimatological methods. The nature of and changes in the microclimate, that set of atmospheric conditions intimately surrounding the individual, have been inadequately studied—a point especially true when the population, rather than the individual, is treated as the unit of observation. Microclimate merits interest because it is the actual climate that influences survival. The scant published data on microclimate suggests that certain discrepancies may exist between gross climatic measurements of the habitat and the prevailing microclimatic conditions to which the individual or population is actually being exposed (Uvarov, 1931; Wellington, 1950, Franklin, 1955).

Certainly the study of the gross climate of habitats has yielded much valuable ecological information concerning the relationship of heat, moisture, and light to the distribution and abundance of animals. The fact, however, that these gross methods may not describe adequately the existing atmospheric conditions to which all animals in a given habitat are exposed may limit their application in some ecological studies. The climate, to which an insect (dwelling upon or inside some plant or animal material) is exposed can be entirely different from the gross atmospheric conditions.

The possible importance of such differences is substantiated by experiments reported in the literature. Poikilothermal animals are usually believed to have the same body temperature as the media in which their bodies are in contact, but this is not always so as pointed out by Gunn (1942) in his comprehensive paper.

The microclimate of phytophagous insects inhabiting a plant has been found to differ from the macroclimate of the same habitat. Studying a habitat in which air temperatures averaged slightly below 24°C, Curtis (1936) found that leaves receiving radiant heat may be 9°C above the ambient air and leaves losing heat owing to radiation may be 4°C below that of the air. The moisture content of the atmosphere may vary as distances from the plant surfaces change. Close (0.5 mm) to a leaf surface the relative humidity may be 93 percent compared to a 52 percent relative humidity 16 mm from the leaf surface (Ramsey, *et al.*, 1938). Thus insects in the microhabitat close to the leaves would be in a measurably different climate than the macroclimatic measurements would indicate.

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[1] This research was conducted while I was a guest investigator at the University of Chicago. I am deeply indebted to Professor Thomas Park for suggesting the study and for his assistance. I am also indebted to Mr. James Bond, Dr. H. M. Johnson, Mr. Monte Lloyd, Dr. C. E. Palm, and Dr. Amelia Polnik.

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An animal population may significantly affect the microclimate in which it lives. Individuals of a population of insects may liberate metabolic heat and moisture to their microhabitat. The importance of this effect upon population survival is exemplified with honey bees. The difference in temperature which may exist between the habitat and microhabitat (hive) is illustrated by the observations of Gates (1914). One February day he recorded −10°C outside the hive and inside the bee cluster a temperature of 30°C, thus a 40°C difference. While this may be extreme, it illustrates the extent to which the climate of the habitat and microhabitat may differ.

Differences between the microclimate and macroclimate may be great and such differences undoubtedly would be of significance to the survival of many species. Other differences may not be as large, and unquestionably many may be ignored. However, the criteria for ignoring the differences between the microclimate and macroclimate should be based on actual experimental data.

The present study deals with just one phase of the many questions concerning microclimate and animal ecology, that is investigating the alteration of the microclimate by an animal population. Animals liberate metabolic heat, and generate some heat owing to other activities such as fraction-heat resulting from movement. Moisture is given off by transpiraion and excretion. Specifically, this study measured the increase of temperature and moisture contributed by an animal population of known density to its microhabitat.

METHODS

The animals used in the study were two granivorous insect species, *Tribolium confusum* and *Tribolium castaneum.* The food consisted of 95 percent single-sifted whole wheat flour and 5 percent yeast. The physical structure of the microhabitat was a shell vial 9.5 cm high and 2.5 cm in diameter, containing 8 grams of the flour-yeast medium. To maintain limited control over the gross climatic conditions, these populated vials were placed in a water bath. The water bath in turn was placed in a constant temperature incubator (29.0 ± 0.5°C) in which relative humidity was held fairly constant (70 ± 5 percent) and from which light was excluded.

Since the microhabitat was small (8 grams of flour) and the population density was relatively low (varying by design between 100 and 300 specimens) the changes imposed by the populations upon the microhabitat were anticipated to be small. Apparatuses, sensitive enough to measure such changes, were developed. The apparatus measuring temperature changes was constructed with a thermistor and wheatstone bridge (Figure 1). This apparatus had a sensitivity of 0.02°C. To measure the temperature of the medium the sensitive portion of the termistor (1 mm in diameter) was inserted into the center of the medium. The humidity measuring apparatus was constructed following the original circuit of Dunmore (1938) and the modification used by Rogers (1956) (Figure 2). This instrument measured the rate of flow of current across a moisture sensitive bridge which was composed of a mixture of polyvinyl acetate and lithium chloride. A galvanometer that had a current sensitivity of 0.03 microamperes per mm division was used. The apparatus had a sensitivity of 0.5 percent relative

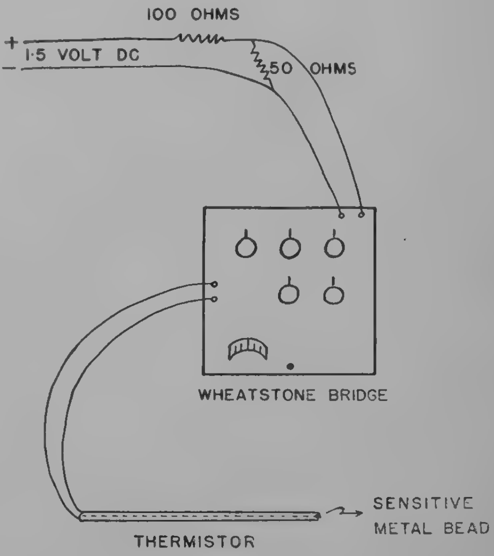

FIG. 1. Diagram of temperature measuring apparatus.

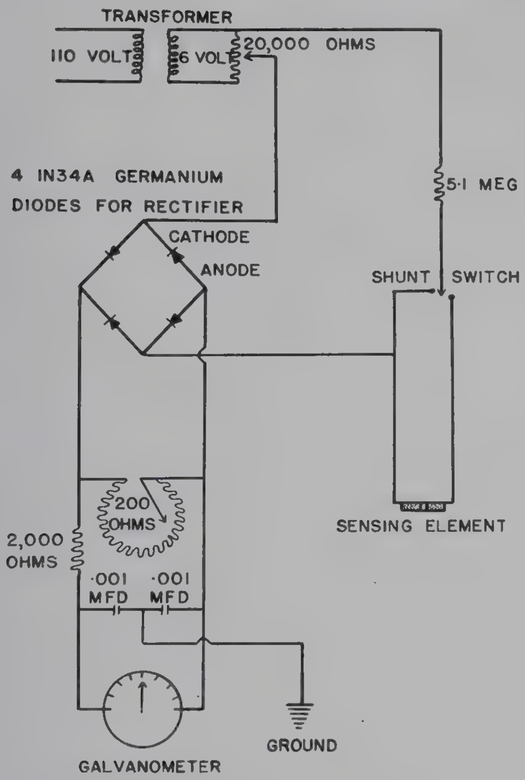

FIG. 2. Diagram of humidity measuring apparatus (after Rogers, 1956).

humidity. In measuring the humidity of the microhabitat the sensitive portion of the "humistor" (1 by 2 mm) was inserted centrally by depth in the flour medium but just to one side of the themistor.

EXPERIMENTAL DESIGN AND RESULTS

Temperature

To determine if *Tribolium* populations do impose a temperature change upon their microhabitat, 300 individuals of each of three different stages for each of two species were maintained in the microhabitat. The test populations contained both *Tribolium confusum* and *Tribolium castaneum* and were made up from strains maintained at the Hull Zoological Laboratory. The adults were of unknown age; the estimated sex ratio was 1 to 1. The larval populations consisted of small, medium, and large larvae in 3 : 2 : 3 ratio, respectively. This 3 : 2 : 3 ratio approximated the ratio of small, medium, and large larvae usually found in an average population in this particular microhabitat (Park, 1954).

These experimental microhabitats, consisting of insects plus medium, and the controls (medium alone) were replicated 24 times. The insects were left in the new microhabitats for 24 hours before the initial temperature measurement was made, since preliminary tests indicated that maximum temperature rises occurred by the 24th hour.

The temperature in the microhabitats containing insects regardless of species or stage was significantly greater (at the 1 per cent level) than the temperature of the microhabitats without insects (Table I). Differences in temperature rise imposed by the population of different species upon the microhabitat was not statistically significant.

TABLE I. The increase in temperature imposed by 300 specimens of each of three stages of *T. confusum* and *T. castaneum* upon their microhabitat. Each test replicated 24 times

Species	Stages	EXPERIMENTAL Mean Temp. ± S. E.	CONTROL Mean Temp. ± S. E.
T. confusum	adult	29.30 ± 0.011	29.00 ± 0.005
	pupal	29.13 ± 0.005	29.00 ± 0.007
	larval	29.55 ± 0.028	29.00 ± 0.004
T. castaneum	adult	29.33 ± 0.018	29 00 ± 0.008
	pupal	29.08 ± 0.014	29.00 ± 0.008
	larval	29.60 ± 0.074	29.00 ± 0.003
T. confusum plus *T. castaneum*	adult	29.37 ± 0.009	29.00 ± 0.004
	pupal	29.10 ± 0.016	29.00 ± 0.015
	larval	29.44 ± 0.032	29.00 ± 0.010

When three stages of *T. confusum* and *T. castaneum* were combined in a 1 to 1 ratio, the temperature in the microhabitat was not greater than that imposed by either of the two species measured separately (Table I).

To determine the biomass of each stage for both *T. confusum* and *T. castaneum,* 24 lots each for larvae and adult stages and 12 lots each for the pupal stage were weighed. Each lot consisted of 300 specimens. The biomass of 300 specimens of each of the three stages of *T. confusum* and *T. castaneum* are presented in Table II. While the quiescent pupae weighed more than either adults or larvae of like population size, they caused only slight increases in temperature compared to the increase attributed to the larvae and adults (Tables I and II). All stages of *T. confusum* were significantly heavier than the corresponding stages of *T. castaneum.* As mentioned previously, however, the differences between species in imposed temperature increases were not statistically significant. Thus, there seemed to be little, if any, association between the biomass and temperature increase imposed upon the microhabitat by these various populations.

TABLE II. The biomass of 300 specimens of each of three stages of *T. confusum* and *T. castaneum*

Species	Stages	300 Specimens Gram Weight ± S.E.	1 Specimen Avg. Gram Weight
T. confusum	adult	0.6776 ± 0.00480	0.0023
	pupal	0.7645 ± 0.01570	0.0025
	larval	0.4885 ± 0.02459	0.0016
T. castaneum	adult	0.5928 ± 0.00577	0.0020
	pupal	0.7379 ± 0.01065	0.0025
	larval	0.4205 ± 0.02943	0.0014
T. confusum plus *T. castaneum*	adult	0.6204 ± 0.00723	0.0021
	pupal	0.7629 ± 0.03577	0.0025
	larval	0.5565 ± 0.03094	0.0019

Three hundred adult *Tribolium* of unknown age and having an estimated sex ratio of 1 to 1 were placed into each test microhabitat. Populations of *T. confusum* and *T. castaneum* were first tested separately and then populations consisting of a combination of both species in a 1 to 1 ratio were studied. Temperature measurements were made after 8 hours elapsed time and were repeated daily thereafter at 0800, 1600 and 2400 hours for the four-day test period. The three experimental groups and one control were each replicated 12 times.

If a comparison is made between the data presented in Table I and Figure 3 (24-hour point on abscissa) a slight difference in temperature increase for the various specific populations will be noted. This difference results from the times at which temperature measurements were made; measurements presented in Table I were read about 1600 hours (afternoon) while measurements presented in Figure 3 were read during early morning 0800 hours.

The temperature of all the media containing test populations increased rapidly and reached a peak within 24 hours. The temperature then declined rapidly during the second 24 hours, and thereafter continued a slow decline to a level below the initial temperature. The *T. confusum* populations produced a slightly higher temperature rise than the *T. castaneum* populations; the populations of a mixture of the two species were approximately intermediate. These differences, however, were not statistically significant. A comparison of the temperature of the microhabitat at 16 and 96 hours indicated a significant (0.01) decline in temperature by the 96-hour point.

Informal observations indicated that the number of beetles submerged in the medium and found on the surface varied with both time and "conditioning" (assumed to be the increase in concentration of toxic wastes) of the medium. To

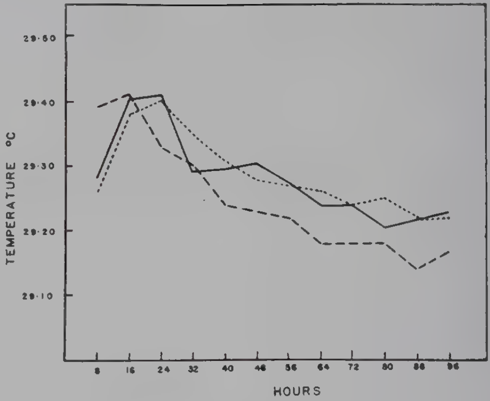

FIG. 3. Temperature increase above a control temperature of 29.00°C imposed by *Tribolium* populations upon their microhabitat at various periods of time after placement in fresh medium. Each point is an average of 12 replicates. Solid lines are are *T. confusum* at a density of 300; broken lines, *T. castaneum* at a density of 300; dotted lines, *T. confusum* and *T. confusum* together each at a density of 150.

study this possibility, 30 replicates composed of 300 individuals of each species and combination of two species (1:1 ratio) were tested using adult population groups similar to those in the previous temperature measurements. In the 30-replicate group a count of the number of beetles present on the surface of the medium for each of these replicates were made at 32 hours and 96 hours after insects were introduced into the microhabitat. The counts were made between 0900 and 1200 hours. Subsequently, additional tests using 40 more replicates for each of the two species were made. In this test the 40 replicates were examined for the number of beetles on the surface about 168 hours (7 days) later. At this time 20 replicates for each species were examined at 0900 (morning) and the remaining 20 were examined at 2100 hours (evening). For all tests, each replicate was removed from the darkened incubator individually and the beetles on the surface aspirated off quickly. Special care was taken to allow very little light to enter the incubator when the sampling was in progress.

A notable difference in the vertical distribution of *Tribolium* took place with time and "conditioning" of the medium (Table III). Significantly (0.001) more *T. confusum* were present on the surface at 32 hours than at 96 hours; and a significantly (0.005) greater number were on the surface at 168 hours than at either 32 or 96 hours. Note that readings taken at 32, 96 and 168 hours were all morning readings. For *T. castaneum* the

TABLE III. Mean number of *Tribolium* found on the surface of the medium 32, 96, and 168 hours after initial introduction of 300 specimens each of *T. confusum* and *T. castaneum* and 300 of both species in a 1:1 ratio into fresh medium

T. confusum	NUMBER ON SURFACE OF MEDIUM AT VARIOUS TIMES			PROBABILITY OF REAL DIFFERENCES BETWEEN OBSERVATION AT DIFFERENT HOURS		
Species	32 hrs.	96 hrs.	168 hrs.	32 vs. 96	32 vs. 168	96 vs. 168
T. confusum.........	89*	72*	190†	0.001	0.005	0.0001
T. castaneum.........	62*	153*	141†	0.0001	0.0001	NS
Probability of *T. confusum* vs. *T. castaneum*.........	0.005	0.0001	0.0001			
T. confusum + *T. castaneum*........	81*	104*	......	0.001		
(Broken down)						
T. confusum.........	40	34	......	0.01		
T. castaneum.........	41	70	......	0.0001		

*Average of 30 replicates. †Average of 20 replicates.

pattern of migration was different; few beetles were on the surface at 32 hours. At both 96 hours and 168 hours at least twice as many beetles were on the surface of the medium as were found at the 32-hour check. The combination of species was essentially intermediate with each species in the group reacting typically as a member of a single species population. Thus a significantly greater number of *T. confusum* were on the surface at 32 hours compared to *T. castaneum*. At 96 and 168 hours a significantly greater number of *T. castaneum* were on the surface than *T. confusum*. These data may explain why habitats containing *T. confusum* populations had indicated higher temperatures than *T. castaneum* as time elapsed, since more *T. confusum* individuals were in the medium as time passed compared to the number of *T. castaneum*. However, the vertical migration data do not suggest any reason for the decline in habitat temperature which occurred after the 24th hour. Although *T. confusum* was entering the medium and *T. castaneum* was coming out, the temperatures of the microhabitats containing each species continued to decline. Possibly, as more permanent tunnels were constructed and the beetles become "accustomed" to their microhabitat, their energy output decreased with a corresponding temperature decline.

In the group which was held 168 hours a search was made for a daily vertical-migration rhythm, and as indicated by many preliminary observations and by the data in Table IV, such a daily rhythm does occur. A significantly greater number of beetles of both *Tribolium* species were on the medium surface at night than during the morning.

TABLE IV. Mean number of a population of 300 specimens of *T. confusum* and *T. castaneum* found on the surface of the medium at 0900 hours and 2100 hours on the 7th day after initial introduction

	MORNING		NIGHT		PROBABILITY		
						♂♂ vs. ♀♀	
Species	No.	Sex ♂;♀	No.	Sex ♂;♀	Morning vs. night	Morning	Night
T. confusum	109	1.3:1	135	1.1:1	0.0001	ns	ns
T. castaneum	141	1:1	169	1:1	0.0001	ns	ns
Probability *T. confusum* vs. *T. castaneum*	0.0001	.....	0.0001				

No difference between the two sexes occurred in this vertical migration. The difference between *T. confusum* and *T. castaneum* in number of individuals on the surface was significant at both the morning and night measurements. The effect of this vertical migration upon the daily temperature pattern was clarified in the following experiment.

A measurement was made of the temperature increase imposed by adult male and female *T. castaneum* populations upon their microhabitat during a 16-day period. Each sex was measured with the following population densities for each sex and the controls (medium alone) were replicated 6 times. The beetles were about 2 days old when introduced into the medium. Temperature measurements commenced 12 hours after the beetles were introduced and thereafter twice each day at 0900 and 2100 hours for the entire 16-day period.

For the first 24 hours, and then to a lesser extent thereafter, a positive association was indicated between the number of beetles in the microhabitat and the temperature increase above the controls (Figures 4 and 5). While a gradual decline in temperature occurred for all densities during a 6-day period following the initial rise, the sharpest decline in temperature occurred in the microhabitats containing populations of the greatest density. After this, temperature readings leveled and remained fairly constant for the remainder of the 16-day test period. Comparing averages of the temperature data for each replicate from 3.5 days through to the 16th day, an analysis of the data indicated the temperature change increase imposed by each was density related (Table V). Both sexes reacted similarly (Figures 4 and 5), although the female populations appear to have induced a slightly higher temperature rise than the males (difference not significant).

The theory that there was a definite daily vertical migration was substantiated by one of the

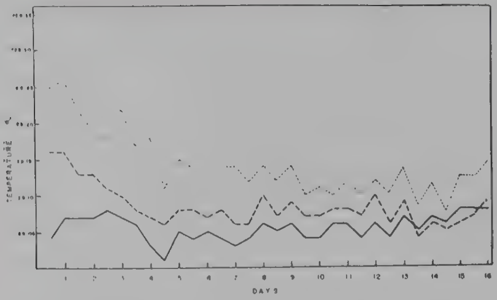

FIG. 4. Temperature increase above a control temperature of 29.00°C. imposed by male *T. castaneus* populations upon their microhabitat at various periods of time after placement in fresh medium. Each point is an average of 6 replicates. Dotted lines are densities of 300; broken lines, densities of 200; solid lines are densities of 100.

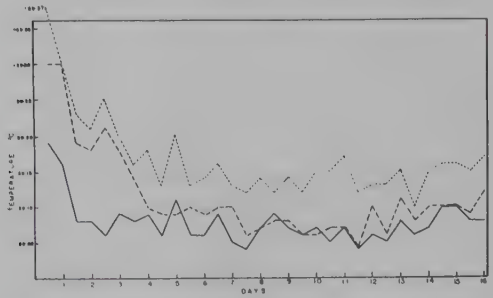

FIG. 5. Temperature increase above a control temperature of 29.00°C. imposed by female *T. castaneum* populations at densities of 300, 200, and 100 upon their microhabitat at various periods of time after placement in fresh medium. Each point is an average of 6 replicates. Dotted lines are densities of 300, broken lines are densities of 200; solid lines are densities of 100.

previously described experiments. This diel migration resulted in a definite pattern of day-night temperature rhythm, generally high temperatures at 0900 (morning) and low temperatures at 2100 hours (night) (Table VI and Figures 4 and 5). What part, if any, the general activity of the beetles had upon the day-night temperature rhythm is not known. The rhythm was best exemplified by populations containing the 300 individuals of both sexes, because the initial temperature increase imposed by these densities was great enough so that the *actual* temperature pattern was less affected by variables inherent in the design. There was more variability in the temperature measurements for the low population densities. Populations consisting solely of females produced more variable data than those of only males.

TABLE V. Temperature increase in microhabitats containing populations of beetles and an analysis of these data. Average temperature of the medium above a control temperature of 29.00°C for sex and the various population densities, replicated 6 times using temperature measurements from 3.5 days through the 16th day. Analysis of variance of the data comparing variation between density and sex, and the interaction of density and sex.

	AVERAGE TEMPERATURES					
	Male			Female		
	Density			Density		
Temperature Data	300	200	100	300	200	100
Morning	29.109	29.069	29.049	29.137	29.078	29.066
Night	29.136	29.080	29.058	29.150	29.096	29.076
Combined	29.122	29.075	29.053	29.144	29.087	29.071

ANALYSIS OF VARIANCE

	ANALYSES OF VARIANCE FOR TEMPERATURE DATA								
	Morning Data Only			Night Data Only			Data Combined		
Source of Variation	DF	MS	P	DF	MS	P	DF	MS	P
Density	2	18,603.5	0.01	2	14,118.5	0.01	2	16,358.0	0.01
Sex	1	2,240.0	0.03	1	2,989.0	0.03	1	2,618.0	0.02
Density & Sex	2	12.5	ns	2	251.5	ns	2	37.0	ns
Within Groups	30	361.4	..	30	513.5	..	30	387.4	..

TABLE VI. A comparison of morning and evening temperatures of the microhabitats to determine the existence of a consistant pattern of higher temperatures in the morning. Three population densities for each of the two sexes were used

Population Density	Sex	Probability (night vs. morning)
300	♂♂	.01
	♀♀	.01
200	♂♂	.05
	♀♀	ns
100	♂♂	.05
	♀♀	ns

Moisture

A measurement was made of the moisture increase imposed by male *T. castaneum* populations upon their microhabitat. The population densities tested were as follows: 100 beetles; 200 beetles; and 300 beetles. Two experimental runs were made using 3 replicates each for every test group including the controls (medium alone). The beetles were about 2 days old when used for the test. Humidity measurements were made initially, 12 hours after the beetles were introduced, and thereafter at 0900 and 2100 hours daily for 16 days. The humidity measurements were made simultaneously with the temperature measurement described previously.

For the first 5 days a rapid increase in moisture occurred in the microhabitat and it was not until the 10th day that the increase generally ceased (Figure 6). Only three replicates were followed for the first 7 days instead of six. The calibrated humistors had a sensitive range of between 65 and 85 percent relative humidity and at 65 percent or slightly below the response of the humistors was poor. During the first experimental run the controls were in this questionable range during the first 7 days and the data were considered unreliable. Therefore, data for the first 7 days are based on only 3 replicates for each test group. At 15.5 days the comparison of the relative humidities of the microhabitats imposed by the three population densities is indicated in Table VII. In this one analysis the difference in moisture increase caused by the 300 and 200 densities is not significant. The number of replicates, however, is considered a limiting factor in this instance. The trends as plotted on the graph certainly indicate a rather consistent relationship between density and moisture increase.

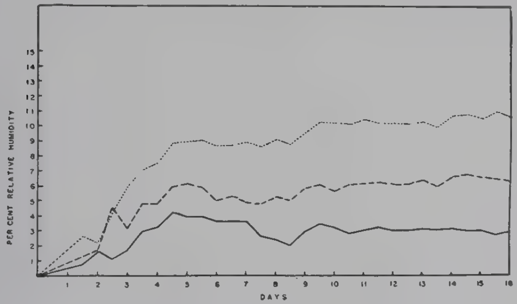

FIG. 6. Relative humidity increase above the controls imposed by male *T. castaneum* populations at densities of 300, 200, and 100 upon their microhabitat at various periods of time after placement in fresh medium. Each point is an average of 6 replicates. Dotted lines are densities of 300; broken lines, densities of 200; solid lines are densities of 100.

TABLE VII. A comparison of the relative humidity increase imposed by male *T. castaneum* populations of various densities upon their microclimate 15.5 days after introduction into the microhabitat

Comparison of Densities	Mean Increase in Relative Humidity	$M\Delta \pm S.E._{M\Delta}$	t	Probability
300 vs. 200	10.67 6.43	4.24 ± 2.42	1.75	ns
300 vs. 100	10.67 2.83	7.84 ± 2.39	3.28	0.001
200 vs. 100	6.43 2.83	3.60 ± 1.68	2.14	0.03

DISCUSSION

The study reported herein substantiates two facts. First, a measurable difference exists between the climate of the habitat and the microclimate of populated flour—the temperature and moisture content of the microhabitat being significantly higher than the temperature and moisture content of the habitat alone. Secondly, this increase in temperature and moisture was generally related to the population density. These experiments demonstrated that microclimate is both of environmental and population origin. The challenge of exploring the relation of this observation to population dynamics still remains.

In the reported experiments the maximum temperature increase measured was less than 1°C and relative humidity increase was about 11 percent. While these changes are not great in themselves, it must be remembered that the physical milieu was 8 grams of a flour-yeast mixture and only relatively small populations (300 individuals or less) were utilized. If microhabitats of larger physical size and containing larger insect populations were located in a medium, such as grain, which could offer nearly complete insulation against moderation of the heat and moisture increase of the microhabitat, differences in moisture and temperature between the microhabitat and ambient air of the habitat could be greater and have a more significant effect upon the population. As mentioned in the introduction, in large stores of grain granivorous insects may heat their microhabitats as high as 25.0°C above that of the macrohabitat.

When temperature and moisture levels of microhabitats containing insects were followed in time, the temperature rose sharply during the first 24 hours and then gradually declined for 6 days to settle at a level just above the controls; the moisture content increased rapidly for the first 5 days and then more slowly until a maximum was reached about the 10th day. As mentioned previously the temperature might have declined as the beetles constructed permanent tunnels and became "accustomed" to their microhabitat, since lowered energy output would be associated with a temperature decline. How long it takes a population of beetles to construct permanent tunnels and what proportion of the population use these tunnels is not known. Even when permanent tunnels were known to be in the microhabitat a few beetles were observed burrowing through the medium. Some association between the moisture level of the medium and the number of tunnels present was observed; more tunnels appeared to be present in moist medium than in less moist medium, perhaps because the moist medium was a factor in the persistence of the tunnel walls. The increased humidity with time may have allowed for more permanent tunnels with less expenditure of energy on the part of the beetles, reflected in a drop in temperature. In general, the decline in temperature which occurred was probably an indication of the "adjustment" of the beetles to their new habitat; it may take 5 to 6 days for the beetles to construct tunnels and become "accustomed" to a new habitat.

The immediate surrounding conditions of heat, moisture, and light to which the organism is exposed (microclimate) are the actual climatic factors influencing the survival of the organism. As instrumentation improves, more sensitive measurements of these factors can be made. Instrumentation is at best only a tool; the importance of the study is to explore the relationship of microclimate to population abundance and distribution. A more exhaustive study of the action of microclimate upon animal populations and the reaction of the animal population upon microclimate should yield cogent ecological information concerning the regulation of animal numbers.

SUMMARY

An investigation was made of the changes in microclimate imposed by populations of *Tribolium confusum* and *Tribolium castaneum* in their microhabitat. The temperatures of the microhabitat containing *T. confusum* and *T. castaneum* populations as either larvae, pupae, or adults were significantly greater than the temperatures of the microhabitats without insects. Populations of 300 larvae raised the temperature 0.60°C above that of the controls. No relationship was found between the biomass of the adult, pupal, and larval stage and the amount of temperature increase imposed by that population. When the temperature changes imposed by adult populations were followed in time, an immediate rise in temperature was noted, with the maximum increase reached in 24 hours. Following this, a general decline in temperature took place for 6 days. A period then commenced in which the temperature remained fairly constant for the remainder of the 16-day test period. The temperature increase in the microhabitats with beetles was density related. Temperature changes measured were influenced in part by a dispersal of the beetles from the surface of the medium into the medium itself. The dispersal pattern was quite different for the two species and appeared related to the "conditioning" of the medium. A second movement, that is, a daily vertical-migration rhythm was observed and this was thought to cause relatively high morning and low night temperatures in the microhabitats.

In a measure of the moisture increase imposed by male *T. castaneum* populations upon their microhabitat, the moisture content was found to increase rapidly for the first 5 days, then more slowly until a maximum occurred about the 10th day. For populations containing 300 adult beetles the maximum rise in relative humidity was 11 percent. The humidity increase in the microhabitats with beetles was generally density related.

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THE SEASONAL DISTRIBUTION OF THE ZOOPLANKTON OFF CHICKEN KEY IN BISCAYNE BAY, FLORIDA

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Introduction

This investigation was undertaken to determine the nature and seasonal distribution of the zooplankton community at a single station off Chicken Key in Biscayne Bay, Florida. Seasonal data on the water temperature, salinity and rainfall were obtained for comparison to the seasonal distribution of the zooplankton.

The plankton station maintained is located at approximately 25° 37′N, 80° 17′W, about one mile east of the irrregular mainland shoreline of mangrove swamps and about one-eighth of a mile east of Chicken Key, which is a mangrove island. The depth at mean low tide for this location is six to seven feet. The station discussed here corresponds to station number eleven of Smith, Williams and Davis (1950), who present a map showing the position of Chicken Key in Biscayne Bay.

Information on the seasonal distribution of zooplankton in south Florida is rather sparse. Some seasonal information on individual plankters is contained in a study of the composition of the plankton of south Florida by Davis (1950), and isolated records on various planktonic species may be obtained from the publications of Davis (1947, 1948, 1949) and Davis and Williams (1950). A brief seasonal plankton study of a quantitative nature has been included by Smith, *et al.* (1950) in their ecological survey of the inshore waters adjacent to Miami.

Acknowledgments are accorded to Charles C. Davis, whose guidance made possible this study, to Hilary B. Moore, who offered many helpful suggestions and to J. Fred Walker, whose interest facilitated the completion of this project. Identification of most of the copepods was either made or confirmed by C. C. Davis, and the species of *Lucifer* was identified by Fenner A. Chace, Jr. The salinity analyses were done by Robert H. Williams. Much of the statistical analysis was done by Mrs. Hazel H. Woodmansee. For assistance in the field work acknowledgments are due my father, Ralph B. Woodmansee, who supplied the outboard motor, George and Richard Kosel, who supplied the skiff, and the Zoology Department and Marine Laboratory of the University of Miami. This project has been partially supported by an A.A.A.S. grant made available through the Mississippi Academy of Sciences.

Method

Daytime samples of surface plankton were procured weekly from October 18, 1947 to December 27, 1948 with a standard open No. 6 plankton net. The net was towed along a prescribed course for a ten-minute period at the same motor speed each time. Under these circumstances the volume of water presented to the opening of the net during each tow should be nearly constant. Since the currents off Chicken Key are thought to be predominantly tidal, and samples were taken at random with respect to tide, an estimation of the average distance traveled during a sampling run permits one to calculate the volume of water presented to the opening of the net with an accuracy which seems to be sufficient for comparison with other quantitative plankton data.

In the calculation of plankton volume concentration, it has been assumed that the straining efficiency or percent filtration of the net is 100 percent throughout the sampling run. This assumption is certainly not completely valid since the straining efficiency of a No. 6 net is probably never 100 percent and is undoubtedly progressively reduced during the course of a sampling run as the mesh becomes clogged with organisms. Therefore, the data presented in terms of plankton volume per cubic meter of water represent minimum concentrations.

Since the rate and degree of net clogging undoubtedly vary with the types of organisms present in the water, minor seasonal fluctuations in plankton concentration could result solely from the inaccuracies of the method. With a source of error of this sort inherent in the method of collection only the major quantitative variations should be considered significant.

In the laboratory the wet volume of each plankton sample was determined by placing the sample in a graduated cylinder and reading the volume occupied by the plankton after a 24 hour settling period. Plankton volumes determined by this settling technique may be divided by four to give an approximate conversion to displacement volumes (Sverdrup, Johnson and Fleming, 1942). When the ctenophore *Mnemiopsis mccradyi* was present in the sample, its living volume was measured in the field with a graduated cylinder because preservation in formalin destroys these animals

TABLE I. Percentage composition of the major elements of zooplankton, plankton volume, temperature, salinity and rainfall off Chicken Key

	November	December	January	February	March	April	May	June	July	August	September	October	November	December	1948 Mean
Gastropod veligers	46	49	39	40	27	37	39	51	35	37	41	6	71	66	41
Copepods	36	34	40	37	43	31	39	39	47	36	28	54	19	26	37
Decapod zoeae	9	4	10	22	27	28	16	3	4	3	22	6	4	4	13
Sagitta	3	5	6	..	2	1	3	3	5	6	1	1	1	1	3
Ceratium	3	5	1	..	..	..	..	..	..	..	..	25	2	..	2
Pelecypod veligers	1	..	1	..	..	1	1	..	1	3	3	4	1	..	1
Echinoplutei	..	..	..	..	..	1	..	1	..	7	2	..	..	..	1
Hydromedusae	1	..	..	..	..	..	..	..	5	4	..	1	..	..	1
Plankton volume (cc/m³)	.53	.98	.33	.53	.41	.45	.53	.41	.11	.24	.18	3.00	.45	.57	.60
Mean temperature (° C)	.....	24.2	20.8	25.0	26.0	24.9	28.4	30.1	30.2	30.2	29.6	26.5	27.6	24.3	27.0
Mean salinity (o/oo)	.....	23.9	26.2	27.1	31.5	34.0	33.2	31.3	33.2	31.6	30.1	20.2	21.6	28.5	29.0
Rainfall (inches)	4.0	2.7	4.6	0.2	2.9	4.3	7.1	7.8	6.4	11.0	21.9	10.7	1.6	1.1	6.6

and leaves the rest of the sample in an unsatisfactory condition. The percentage composition of each plankton sample was determined by counting two hundred organisms selected at random. This counting technique gives only the relative numbers of the various plankters in the community and is not an expression of their actual concentrations. Since a No. 6 net retains very few phytoplankers, this study is essentially restricted to the zooplankton. The only plants enumerated are three species of *Ceratium* which appeared in sufficient numbers to be considered.

As each plankton sample was being taken a measurement of the surface water temperature was made and a surface water sample was obtained for a salinity determination by silver nitrate titration.

The rainfall data are from the Chapman Field Weather Station, which is located on the mainland about two miles northwest of the plankton station.

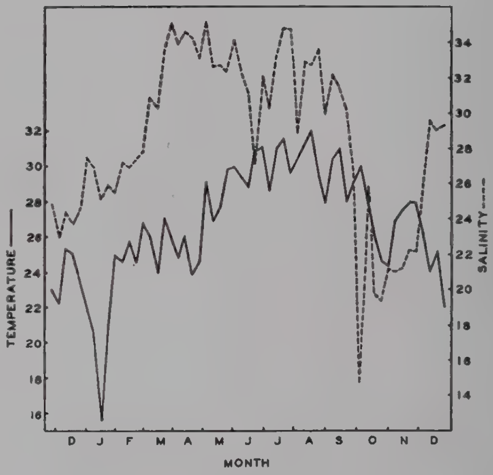

FIG. 1. Surface water temperature in degrees Centigrade and surface salinity in grams per kilogram off Chicken Key.

TEMPERATURE, SALINITY AND RAINFALL

The variations of temperature, salinity and rainfall are shown in Figures 1 and 2. Monthly means for these factors are given in Table I.

The surface water temperature varied from a low of 15.6° C in January to a high of 32.0° C in August with a mean of 26.9° C for the year 1948. Water temperatures dropped rapidly early in January but rose in the latter part of January to maintain a fairly constant level near 25°C through February, March and April. The temperature rose again in May and from June through September oscillated between 28° and 32°C. The water temperature then dropped steadily during October, rose temporarily in November, and then dropped again during December.

The surface salinity varied from a low of 14.8 ⁰/₀₀ in October to a high of 35.1 ⁰/₀₀ occurring in March and May with a yearly mean of 28.0 ⁰/₀₀. From December, 1947, the salinity increased steadily to a maximum monthly average in April, 1948, after which the salinity dropped gradually and irregularly through the late spring and summer showing a secondary maximum in July. Following the heavy rains in late September, the salinity dropped to an annual minimum in early October and remained low through November, rising again in December. Samples were taken at random with regard to the stage of the tide, so that salinity variations caused by the tidal state are included with the seasonal variation in salinity. The tidal state is undoubtedly important in deter-

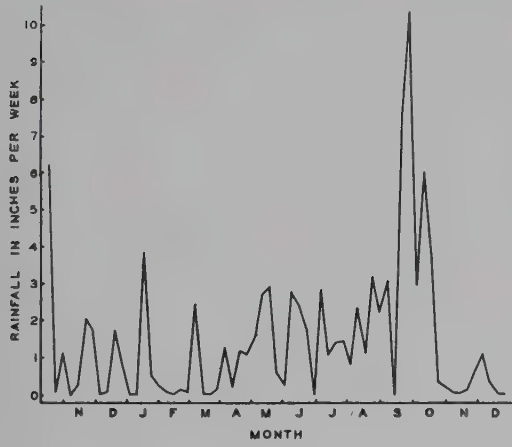

Fig. 2. Rainfall from the Chapman Field Weather Station.

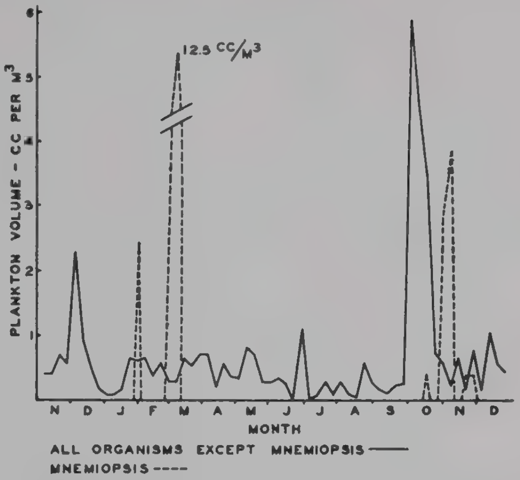

Fig. 3. Plankton volume and volume of *Mnemiopsis.*

mining the salinity, particularly when the salinity is low.

Rainfall data from the Chapman Field Station are shown in weekly intervals. During 1948, 81 percent of the annual rainfall fell during the six-month period from May through October with 55 percent of the annual rainfall occurring during the latter three months of this period. A well-defined maximum in the rainfall curve occurred in the latter half of September. This peak rainfall period, which was associated with two tropical hurricanes, extended into the first part of October.

Plankton Volume

The seasonal distribution of the total plankton volume as sampled with a No. 6 net is shown in Figure 3, and the monthly means are shown in Table I. The volume contributed by the ctenophore *Mnemiopsis mccradyi* has been separated from the volume of the rest of the zooplankton because of its large size and irregular occurrence and because the collecting technique did not permit adequate sampling of these large plankters. A single large *Mnemiopsis* taken in a tow in this study would represent a volume of about lcc/m^3. In the discussion of plankton volume below, the volume of *Mnemiopsis* has been excluded unless a statement is made to the contrary.

The mean plankton volume for the year 1948 was 0.63cc/m^3 and the median plankton volume for the same period was 0.32cc/m^3. Following a peak of 2.3cc/^{3} in the first week of December, 1947, the plankton volume declined to a very low value in the first half of January, 1948. It then increased during the latter half of January to a level which was more or less maintained through the middle of June. This level was slightly less than the mean yearly volume. During July, August and September the plankton volume was at its lowest level. Abruptly following this summer minimum there occurred in the first part of October the single major peak of the year. This well-defined maximum was of about three weeks' duration and was then followed through the end of October, November and December by values of the same order of magnitude as those found in the spring.

The most characteristic features of the seasonal plankton volume curve are, in 1948, the well-defined but brief October maximum following a sustained summer minimum and, in 1947, a very brief maximum in December. Despite the fact that the seasonal data of Smith *et al.* (1950) are very meagre, they do, in agreement with the present study, indicate a fall plankton maximum for the unpolluted southern part of Biscayne Bay.

Composition of the Plankton Volume Maxima

Figure 4 shows the percentage composition of the zooplankton community immediately preceding, during and immediately following the October maximum. The October plankton peak, which attained a volume of 5.9cc/m^3, was made up predominantly of the copepod *Acartia tonsa* with the dinoflagellate *Ceratium fusus* becoming abundant during the second and third week of the peak. Although relatively abundant in numbers, *Ceratium fusus* certainly made only a very minor contribution to the plankton volume. Brachyuran zoeae made a minor contribution to the first week of the plankton maximum while larvaceans contributed slightly to the third week. At the beginning of the peak 91 percent of the *Acartia tonsa* were in

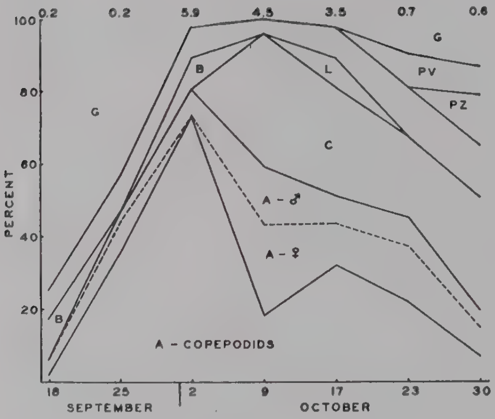

FIG. 4. Percentage composition of the major elements of the Plankton before, during and after the October maximum, which occurred from October 2 through October 17. Across the top of the figure the plankton volumes are given in cubic centimeters per cubic meter. A: *Acartia tonsa*, C: *Ceratium fusus*, G: gastropod veligers, B: brachyuran zoeae, L: larvaceans, PV: pelecypod veligers, PZ: paguridean zoeae.

the copepodid stage with the percentage of adults increasing considerably in the second and third week. Nauplii are not retained by the net employed.

The peak of the first week in December, 1947, was 61 percent *Acartia tonsa,* 15 percent gastropod veligers and 14 percent *Ceratium furca* by number. Seventy-two percent of the *Acartia* were in a copepodid stage and the rest were adult. A minor peak of 1.1cc/m^3 occurring in the last week in June was 66 percent *Acartia tonsa,* 24 percent gastropod veligers and 6 percent *Acartia spinata.* Fifty-three percent of the *Acartia tonsa* were in a copepodid stage. Another minor peak of 1.1cc/m^3 occurring in the second week of December, 1948, was 88 percent gastropod veligers, 4 percent *Acartia tonsa* and 4 percent the copepod *Paracalanus parvus.*

The major contributor to the plankton peaks is certainly *Acartia tonsa,* particularly the copepodid stages of this plankter which is usually abundant at Chicken Key, where it averaged 22 percent of the total nnumber of organisms for the year 1948. Since the *Acartia tonsa* population sampled for the entire year was 52 percent copepodids and 48 percent adult, the two largest peaks show a definitely higher than average number of *Acartia* copepodids.

Mnemiopsis mccradyi appeared in the latter half of January and again during the first part of March when it momentarily became very abundant in the waters off Chicken Key. This ctenophore was encountered again only from mid-October through November becoming a predominant part of the plankton volume for a two-week period covering the last of October and the first of November. Although *Mnemiopsis* feeds upon, and may significantly reduce the quantity of zooplankton (Nelson, 1925; Barlow, 1955), the periodic occurrences of this ctenophore at Chicken Key do not appear to have had any marked influence on the volume of the zooplankton.

COMPOSITION OF THE PLANKTON

Ninety-nine percent of the plankton taken at Chicken Key can be conveniently separated into the eight categories shown in Table I, which shows the percentage composition of the plankton for the 14-month period from November, 1947, through December, 1948, as well as the annual means for 1948. The importance of larval forms in the plankton off Chicken Key is evident.

Gastropod Veligers

This nearshore location is characterized by an abundance of gastropod veligers which are actually more abundant than the copepods. Gastropod veligers made up a farily constant percentage of the plankton for the first eleven months of the study, showing a percentage maximum in December, 1947, a minimum the following March, and a second maximum in June. Then from an average percentage in September, the relative number of gastropod veligers dropped to an annual low of 6 percent in October and reached an annual high of 71 percent the following month. The low in October does not necessarily mean that the absolute number of gastropod veligers decreased during this period, but only that they did not increase proportionately with the other components of the plankton, particularly the copepods, during this month of maximum standing crop.

These data indicate, therefore, that one or more of those elements of the gastropod fauna having planktonic veligers lays eggs throughout the year.

Deevey (1948) found that the gastropod veligers in Tisbury Great Pond showed a late spring or early summer maximum in contrast to Biscayne Bay, where the relative and probably the absolute number remain more or less constant throughout the year.

The Copepod Population

Although the species composition of the copepod population changes seasonally, the entire copepod population makes up a fairly constant percentage of the zooplankton community throughout the year. Copepods were most important in October, 1948, when they constituted 54 percent of the

TABLE II. Seasonal occurrence of the minor elements of the copepod population, *Lucifer faxoni* and species of the genus *Ceratium*. The letter x indicates that the organism is present. The letter e indicates that the animal is carrying eggs. The numbers indicate the percentage of total organisms

	October	November	December	January	February	March	April	May	June	July	August	September	October	November	December
Labidocera scotti	.....	x	x	x	x	x	x	x	x	.....	.....	x	x	x	x
Labidocera mirabilis	.....	.....	.....	.....	x	x	x	x	x	x	.....	.....	.....	x	x
Pseudodiaptomus coronatus	x	x	e	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	e	.....
Temora turbinata	.....	x	x	x	.....	x	.....	.....	.....	.....	.....	.....	x	.....	.....
Calanopia americana	.....	.....	.....	x	x	x	x	x	x	.....	.....	x	.....	.....	x
Euterpina acutifrons	.....	.....	e	e	.....	.....	.....	.....	.....	.....	.....	.....	.....	x	.....
Monstrilla floridana	.....	.....	x	.....	.....	x	.....	.....	.....	.....	.....	.....	.....	.....	.....
Monstrilla reticulata	.....	.....	x	x	.....	x	x	x	x	x	x	x	.....	.....	.....
Lucifer faxoni	.....	x	e	x	x	.....	x	.....	.....	.....	.....	.....	x	x	x
Ceratium fusus	x	2	1	1	.....	.....	.....	.....	.....	.....	.....	.....	24	2	.....
Ceratium furca	x	1	4	x	.....	.....	.....	.....	.....	.....	x	x	x	x	.....
Ceratium macroceros	.....	x	x	x	.....	.....	.....	.....	.....	.....	.....	.....	x	x	.....

zooplankton community and least important the following month when they comprised only 19 percent of the zooplankton community. Since the percentage maximum for copepods occurs during the month of maximum standing crop as determined by volume measurements, the absolute number of copepods must have increased to a well-defined maximum in October.

The seasonal distribution of the more important elements of the copepod population is illustrated in Figure 5, and the seasonal occurrence of those copepods which constitute less than 1 percent of the total copepod population is shown in Table II. When it is possible to do so, the seasonal distribution of individual copepods in Biscayne Bay is compared to their seasonal occurrence at other localities along the east coast of the United States.

Acartia tonsa Dana

Constituted 60 percent of the copepod population in 1948

Temperature Range: 15.6°-32.0°C

Salinity Range: 14.8-35.1 $^0/_{00}$.

Although *Acartia tonsa* is an important part of the copepod population throughout the year at Chicken Key, it was relatively most abundant from June through November or December. During the months of June through November in 1948 this species constituted 81 percent of the copepod population being relatively most abundant during October, when it comprised 94 percent of the copepods. During the months of January through May of 1948, when it was less numerous, *Acartia tonsa* made up 38 percent of the copepod population being least abundant in March when it amounted to only 20 percent of the copepods. In 1948, 64 percent of the adults were females and 36 percent males.

The dominance of this species over other copepods at the Chicken Key Station is in agreement with the findings of Davis (1950), who states that it is the most common copepod in the marine waters of Florida. At Beaufort, North Carolina, Sutcliffe (1948) found that *Acartia tonsa* was the most common copepod of the plankton and was present the year around. Davis (1944) found that this species was generally the dominant animal form in Chesapeake Bay but he does not give seasonal data. In the more northern waters of Block Island Sound, Long Island Sound, Woods Hole Harbor, the open waters off Woods Hole and Tisbury Great Pond, *Acartia tonsa* is generally found to occur during the summer, fall and winter months and to be quite abundant in late summer and early fall (Deevey, 1948, 1952a, 1952b, 1956; Conover, 1956; Fish, 1925; Clark and Zinn, 1937).

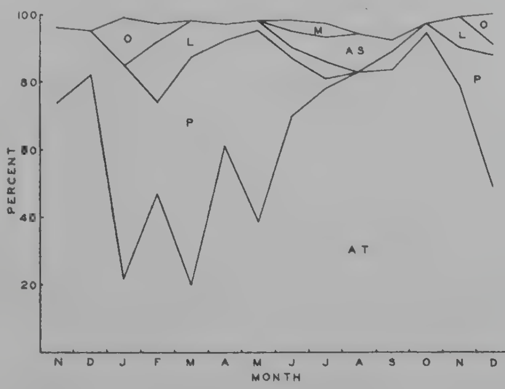

FIG. 5. Seasonal percentage composition of the major elements of the copepod population. AS: *Acartia spinata*, AT: *Acartia tonsa*, L: *Labidocera* copepodid, M: *Metis jousseaumei*, O: *Oithonina nana*, P: *Paracalanus parvus*.

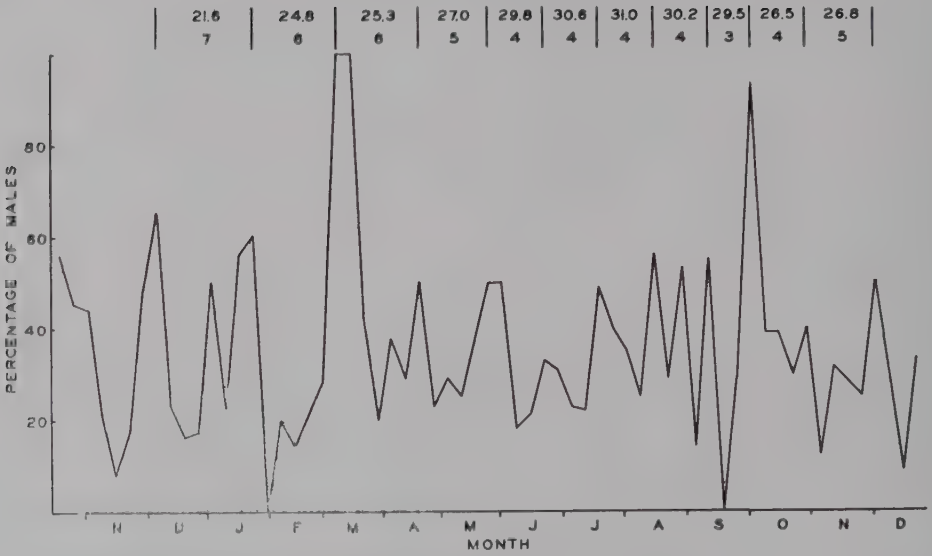

FIG. 6. Seasonal variation in the percentage of males in the adult *Acartia tonsa* population. A somewhat arbitrary selection of major percentage peaks has been indicated by vertical lines across the top of the graph. The time interval in weeks between these peaks is shown between the vertical lines, and just above the time interval is shown the mean surface water temperature for that time interval.

Bigelow (1926) gives Cape Cod as the northern boundary of this species.

In Alligator Harbor *Acartia tonsa* is the second most abundant copepod and occurs throughout the year, being numerically most abundant from August to October and most abundant percentagewise from October to January (Grice, 1956).

Acartia tonsa is accordingly a very abundant copepod in the inshore waters from Cape Cod to Alligator Harbor, Florida. The fact that this species is most abundant during the summer and fall in the waters of both southern Florida and southern New England suggests the lack of any direct influence of the temperature on the success of this species.

The continual presence of adults of both sexes of *Acartia tonsa* suggests that this species breeds throughout the year in Biscayne Bay. Bogorov (1939) has shown that as a rule female copepods are more numerous than males. He has further shown that in the copepodid stages IV and V the number of females is actually a little less than the number of males for the copepods *Pseudocalanus elongatus* and *Metridia longa;* whereas the adults, particularly of *Pseudocalanus elongatus,* show a much higher number of females than males. He accordingly postulates an equal survival of males and females until the adult stage with a subsequent mass mortality or reduced longevity of adult males. Campbell (1934) has observed in *Euchaeta japonica* a rapid dying off of males after fertilization. Clarke (1940) states that the adult males of *Calanus finmarchicus* occur only in January and in May and June and that their appearance presages the commencement of breeding activity.

If this characteristic of copepod life history is applicable to *Acartia tonsa,* a relatively high percentage of males should occur each time that a brood of copepodids becomes adult. In Figure 6 the percentage of males in the adult *Acartia tonsa* population has been plotted against time. Even assuming a reduced longevity of males, it is not possible to determine which of the peaks of males might apply to broods of successive generations and which might apply to secondary broods produced by a given generation. However, Deevey's (1948) data indicate that *Acartia tonsa* produces two broods per generation with the second brood being of a lesser magnitude than the first. Therefore, a somewhat arbitrary selection of major peaks has been made in an attempt to establish the time interval between successive generations. The time interval in weeks between these selected peaks is shown across the top of the graph, and just above the inferred time interval is shown the mean surface water temperature for that time interval. Those peaks of males which have not been selected are for the most part the minor ones, which may represent the appearance of adults of a secondary brood of a given generation and not a subsequent generation.

The inferred time intervals show a decrease in length from winter to summer and a slight increase in the fall, in agreement with the well-known influence of temperature on growth rate. In Figure 7 the inferred time intervals for successive generations are plotted against the mean water temperature during these intervals. With the exception of two points, the inferred time interval is clearly related to the temperature with the interval decreasing as the temperature increases.

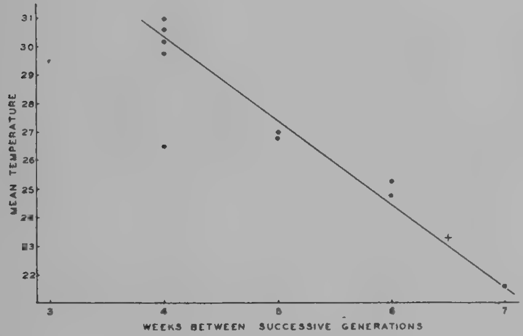

Fig. 7. The proposed time intervals for successive generations of *Acartia tonsa* plotted against the mean surface water temperature for these intervals. The point marked with crossed lines is taken from the data of Deevey (1948).

In Tisbury Great Pond Deevey (1948) suggested a period of six or seven weeks for the development of *Acartia tonsa* during a summer period when the mean water temperature was 23.3° C. This point is plotted on Figure 7 as a cross and is in very good agreement with the data from Chicken Key.

These data suggest that *Acartia tonsa* breeds throughout the year off Chicken Key producing about eleven generations a year and producing second broods within at least some of the generations, and that the time interval between successive generations varies from four to seven weeks. The inferred four-week intervals between successive generations occur during the summer months when the water temperatures are 30° C or over, and the seven-week interval occurs in December and January when the water temperature averages 21.6° C.

The two points which are displaced to the left of the line shown in Figure 7 indicate developmental periods which are shorter than would be expected on the basis of water temperature. These two points represent the three-week generation which developed during September and gave rise to the pronounced October maximum and the generation immediately following it. The apparent more rapid development of these two generations might be the result of a markedly increased food supply. In this connection Marshall and Orr (1952, 1955) have shown that fed *Calanus* mature more quickly and lay more eggs than do starved ones. As will be pointed out later, it seems probable that *Acartia tonsa* and other zooplankters are limited throughout the year by a low quantity of phytoplankton (Smith *et al.*, 1950) and that the October zooplankton maximum is the result of a phytoplankton bloom in late September.

Grice (1956) suggests a twelve-month propagation of *Acartia tonsa* in Alligator Harbor but does not attempt to estimate the number of generations per year. Conover (1956) suggests that there are four generations per year in Long Island Sound.

Paracalanus parvus (Claus)

Constituted 27 percent of the copepod population in 1948

Temperature Range: 15.6°-32.0° C
Salinity Range: 14.8-35.1 ‰

Paracalanus parvus also occurred throughout the year although it was most prominent in the copepod population from the latter part of November until mid-June. During the months of January through May in 1948 *Paracalanus parvus* averaged 49 percent of the copepod population, being relatively most abundant in March when it constituted 67 percent of the copepods. During the summer and fall months of June through November in 1948 this species made up only 7 percent of the copepod population, becoming least important in August when it constituted less than 1 percent of the copepods.

Paracalanus parvus is a widespread species which seems to exist equally well in oceanic and neritic regions. Along the east coast of the United States this species is recorded as being common throughout the year at Beaufort (Sutcliffe, 1948), present all year in Chesapeake Bay (Wilson, 1932b), occurring from July through January with highest numbers in August in Block Island Sound (Deevey, 1952a, 1952b), present from July to December at Woods Hole (Fish, 1925) and present throughout the year, but more abundant in the summer and early autumn months, in the Gulf of Maine (Bigelow, 1926).

In the more northern latitudes then, *Paracalanus parvus* is essentially a summer and fall species, whereas in the warmer waters of Biscayne Bay it is most prominent in the winter and spring. This sort of latitudinal shift in temporal distribution suggests a direct influence of temperature levels on the success of this species.

Together, *Acartia tonsa* and *Paracalanus parvus* made up 87 percent of the copepod population in 1948 with the former species being dominant in the summer and fall and the latter replacing a considerable quantity of the *Acartia tonsa* population in the winter and spring months. In order to determine the effects of temperature and salinity on the relative abundance of these two copepods, a ratio of the percentage of *Acartia tonsa* divided by the combined percentage of *Acartia tonsa* and *Paracalanus parvus* has been calculated for each month. Correlation coefficients for these ratios and the mean monthly temperatures and salinities are —0.14 for the ratio and the salinity of the same month, +0.67 for the ratio and the temperature of the same month and +0.71 for the ratio and the temperature of the previous month. The correlation coefficient for salinity is insignificant. The two coefficients for temperature are statistically significant to the 2 percent level of probability. From an examination of these values it appears that temperature is the factor which is influencing the relative numbers of the two copepods, and that *Acartia tonsa* is most prominent during the period of high water temperatures and *Paracalanus parvus* is particularly numerous during the cold months. Figure 8 illustrates the relationship between the relative abundance of these two copepods and the temperature for the previous month.

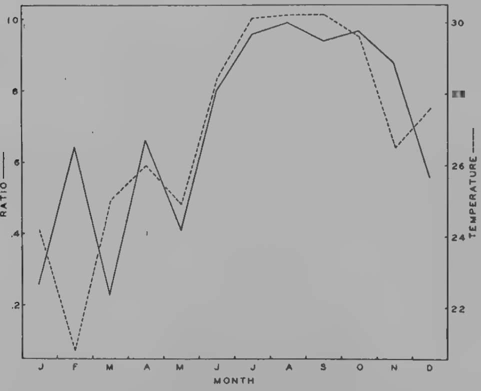

Fig. 8. Seasonal variation of the ratio of the percentage of *Acartia tonsa* over the combined percentages of *Acartia tonsa* and *Paracalanus parvus* and the seasonal variation of the temperature with the temperature curve displaced to the right one month to permit comparison of the ratio to the temperature of the previous month.

These findings are in accord with the facts that both species are fairly euryhaline and that the geographical range of *Paracalanus parvus* extends considerably farther north than that of *Acartia tonsa,* suggesting that where the two species occur together, *Paracalanus parvus* will be the more successful during the colder months.

The fact that the ratio shows significant correlation with the temperatures of both the same and the previous month suggests the importance of the effect of the temperature on either the immature stages or the reproductive activity of these two species.

Labidocera spp. copepodids

Constituted 5 percent of the copepod population in 1948

Labidocera copepodids were present throughout the year, but were relatively most abundant in February, March and November and least important from the latter part of July through October. It is not possible to identify these copepodids since there were two species of *Labidocera* which occurred regularly throughout most of the year. These were *Labidocera scotti* Giesbrecht and *Labidocera mirabilis* Fleminger. Since *Labidocera scotti* was the more abundant of the two and was most prominent during the period of maximum numbers of *Labidocera* copepodids, it would appear that most of the copepodids were *Labidocera scotti.* Adult *Labidocera scotti* occurred in small numbers from September through mid-June being most abundant early in February and completely absent from the plankton from the latter part of June through August when water temperatures were at a maximum. At Chicken Key, adult *Labidocera scotti* exhibited a temperature range of 15.6°-30.4° C and a salinity range of 19.3-35.1 $^0/_{00}$. *Labidocera scotti* has been recorded from Biscayne Bay in December by Davis (1950) and from the Gulf of Guinea by Giesbrecht and Schmeil (1898). Fleminger (1957) gives the distribution of this calanoid in the Gulf of Mexico, and states that it is representative of the tropical or near-tropical coastal area.

Adult *Labidocera mirabilis* occurred from late November through mid-July exhibiting a temperature range of 22.0°-31.0° C and a salinity range of 22.1-35.1 $^0/_{00}$. *Labidocera mirabilis* was originally described by Fleminger (1957), who lists it from the easternmost portion of the Gulf of Mexico in the Key West area.

Oithonina nana (Giesbrecht)

Constituted 3 percent of the copepod population in 1948

Temperature Range: 15.6°-32.0° C
Salinity Range: 14.8-35.1 $^{0}/_{00}$

This small cyclopoid is probably not adequately sampled by a Number 6 net. Although *Oithonina nana* is present throughout the year, it is rather definitely a winter form being most abundant from December through February and achieving maximum numbers in mid-January. Wilson (1932a) records this species from Buzzards Bay in July. Grice (1956) found that *Oithonina nana* occurs more or less throughout the year with maximum abundance in June in Alligator Harbor.

Davis and Williams (1950) record a single specimen of *Oithonina nana* from Onion Key Bay in a salinity of 3.1 $^{0}/_{00}$ and larger numbers from Sunday Bay, where the salinity was 7.2 $^{0}/_{00}$, and Davis (1950) records it as abundant 16 miles offshore in the Gulf of Mexico. It would accordingly appear that the salinity range encountered by this species off Chicken Key was in no way restrictive.

Acartia spinata Esterley

Constituted 2 percent of the copepod population in 1948

Temperature Range : 24.6°-32.0° C
Salinity Range: 28.8-34.8 $^{0}/_{00}$

Acartia spinata is a summer form at Chicken Key occurring only from the latter part of April to mid-September and being most abundant from the latter part of June to the first part of September. In the Miami area Davis (1950) found *Acartia spinata* to be characteristic of the open water just east of Miami Beach, Biscayne Key and Elliot Key with its occurrence in Biscayne Bay restricted to the eastern edge of the Bay. He records this species as being common from June through September, but as occurring from March through November. It would appear, then, that *Acartia spinata* has its population center located in the more open waters, but that its range extends into the western part of Biscayne Bay during the summer months when the salinity and temperature are high and comparable with the conditions in more open water, and when the *Acartia spinata* population is at its maximum. *Acartia spinata* is also more numerous in the offshore waters of Bermuda (Clarke, 1934).

Metis jousseaumei (Richard)

Constituted 1 percent of the copepod population in 1948

Temperature Range. 15.6°-32.0° C
Salinity Range: 22.2-35.1 $^{0}/_{00}$

Metis jousseaumei was of very regular occurrence throughout the year at Chicken Key being most prominent from mid-June to mid-July. Fish (1925) lists this species as one of the most common summer copepods at Woods Hole, where it occurs from June through October. Fish records this copepod as *Ilyopsyllus sarsi,* which is a synonym of *Metis jousseaumei* (See Gurney, 1927). Grice (1956) records this species from Alligator Harbor in August. Wilson (1932a) states that *Metis jousseaumei* has been found in waters varying from a salinity "equal to that of the ocean down to a mere trace" in the Woods Hole area.

Pseudodiaptomus coronatus Williams

Temperature Range: 22.2°-27.5° C
Salinity Range: 21.2-24.4 $^{0}/_{00}$

This species was found at Chicken Key from late October through December. Females with egg sacs occurred in November and December in water tempeartures from 25.0-27.5° C and in salinities which are the same as those given for the species in general. Davis (1948) encountered actively breeding *Pseudodiaptomus coronatus* in June in Long Lake, where the salinity was 15.4 $^{0}{}_{00}$. Davis (1950) also records this species in September and November in the South Florida area. Sutcliffe found *Pseudodiaptomus coronatus* infrequently in July and from October to December at Beaufort. Wilson (1932b) states that in Chesapeake Bay this species is definitely a winter form but is sometimes present at other seasons. At Woods Hole *Pseudodiaptomus coronatus* occurs throughout the year though most abundantly from August through January and exhibits a tall maximum during which it outnumbers all other forms (Fish, 1925). In Long Island Sound *Pseudodiaptomus coronatus* occurs from June through March with maximum numbers from July to November (Deevey, 1956). Grice (1956) records this species from March through December at Alligator Harbor. This copepod was originally described from Rhode Island (Williams, 1906) and has been reported from Nova Scotia (Willey, 1923).

The occurrence of *Pseudodiaptomus coronatus* off Chicken Key from October through December is in fairly good agreement with the seasonal distribution of this species all along the east coast of the United States, where it exhibits a fall or winter maximum. The similar seasonal distributions of this species at different latitudes suggest that its success is not influenced by the prevailing temperature. This calanoid is of more frequent occurrence and apparently much more abundant at Woods Hole than off Chicken Key.

Temora turbinata (Dana)

Temperature Range: 15.6-26.8° C
Salinity Range: 21.3-27.7 ‰

This species occurred irregularly from the latter part of October through the first part of March off Chicken Key. Davis (1950) lists *Temora turbinata* as common in December in the Gulf of Mexico at distances varying from 10 to 60 miles off shore. He also reports the occurrence of this calanoid from September through December in the general area from the extreme eastern edge of Biscayne Bay to a location 2 miles to the east in the Atlantic Ocean. It accordingly would appear that *Temora turbinata* is essentially an open water form and that its occurrence off Chicken Key represents the inshore edge of its normal range. The fact that only very small numbers of these copepods were encountered off Chicken Key suggests that it did not complete its life history in this area.

Grice (1956) recorded *Temora turbinata* from September through January with maximum numbers in October and November in Alligator Harbor. Sutcliffe (1948) encountered *Temora turbinata* from July through November at Beaufort. Wilson (1932b) found this plankter present in abundance during autumn and winter in the outer part of Chesapeake Bay. Deevey (1952a, 1952b) recorded *Temora turbinata* from September to December in Block Island Sound, where it is looked upon as an offshore and southern form. The northernmost records of *Temora turbina* appear to be those of Wilson (1932a) and Bigelow (1926), who report it from Georges Bank in September, February, and April.

Calanopia americana Dahl

Temperature Range: 15.6-31.0° C
Salinity Range: 25.1-35.1 ‰

Calanopia americana occurred from mid-December to mid-June and in September off Chicken Key. Davis (1950) found this form up to 60 miles off shore in the Gulf of Mexico and from the western half of Biscayne Bay to the Florida Current. Although he records *Calanopia americana* in Biscayne Bay during the months of April, August, October, and December, his record in October is for the eastern half of the Bay. Apparently *Calanopia americana* occurs in some part of Biscayne Bay throughout the year with its absence from the western half of the Bay in October and November being perhaps ascribable to the low salinities occurring there during these months.

Dahl (1894) originally described *Calanopia americana* from the coast of Brazil near the mouth of the Amazon River. At Bermuda this species is the dominant copepod inside the reefs (Esterley, 1911; Clarke, 1934), occurring only as an occasional straggler outside (Moore, 1949).

Euterpina acutifrons (Dana)

Temperature Range: 15.6-27.9° C
Salinity Range: 22.2-26.9 ‰

Euterpina acutifrons is a winter copepod off Chicken Key occurring from mid-November to mid-January. Females with ovisacs were encountered in December and January in water temperatures ranging from 15.6 to 22.2° C and in salinities ranging from 23.0 to 25.1 ‰. Davis (1950) finds this harpacticoid occurring commonly in the western part of Biscayne Bay in November as well as in the Florida Current in October and notes its presence in the more open waters of the Miami region from August through December. Grice (1956) finds that *Euterpina acutifrons* occurs throughout the year at Alligator Harbor, where it shows no particular seasonal trend. Dahl (1894) lists this species from the coast of Brazil.

Monstrilla floridana Davis

Temperature Range: 24.0-26.8° C
Salinity Range: 23.7-30.3 ‰

Monstrilla floridana occurred off Chicken Key in December and March. Davis (1949, 1950) originally described this species from Chicken Key and lists it elsewhere in Biscayne Bay in March and May.

Monstrilla reticulata Davis

Temperature Range: 20.5-31.0° C
Salinity Range: 23.0-35.1 ‰

Monstrilla reticulata occurred from December to mid-September and was most prominent in the plankton in June. Davis (1949, 1950) originally described this species from Chicken Key and records it from other parts of Biscayne Bay.

Other plankters

Decapod Zoeae

The decapod zoeae constituted thirteen percent of the zooplankton community in 1948. These larval forms made up more than 20 percent of the zooplankton during a three-month period from February through April and later in September. The early spring maximum was made up of nearly equal numbers of brachyuran, paguridean, and caridean zoeae, whereas the September maximum was almost exclusively brachyuran zoeae.

Sagitta

Immature *Sagitta* occurred throughout the year and constituted 3 percent of the zooplankton. They were most important to the plankton community in mid-winter and mid-summer. Mature *Sagitta* were never abundant but occurred regularly from October through March with none being encountered in the late spring or summer months.

Ceratium

Three species of this genus of dinoflagellates occurred at Chicken Key from August through January. The seasonal occurrence of these species is shown in Table II. The occurrence of these forms in the fall off Chicken Key is consistent with their seasonal distribution in more northern inshore regions.

Ceratium fusus (Ehrenberg)
Temperature Range: 15.6-30.0° C
Salinity Range: 14.8-25.8 $^0/_{00}$

Ceratium fusus occurred from October through January being most abundant during the month of October, 1948 (see Figure 4). The data which Davis (1950) presents for the seasonal distribution of *Ceratium fusus* in the Florida area indicate that it is a fall and winter form, but he also records it in March near Key Largo, and Davis and Williams (1950) record this plankter from Florida Bay in May. These findings are in fairly good agreement with those of Fish (1925) who records this species at Woods Hole from August through December with maxima in October, 1922, and December, 1923; and Johnson (1932), who found that *Ceratium fusus* occurred in Friday Harbor from June through March, reaching maximum numbers in October. In oceanic regions *Ceratium fusus* was found occurring in waters with temperatures ranging from 2.1° to 29.5° C and salinities of 32.7 to 37.0 $^0/_{00}$ (Graham and Bronikovsky, 1944).

Ceratium furca (Ehrenberg)
Temperature Range: 15.6-31.2° C
Salinity Range: 21.0-32.9 $^0/_{00}$

Ceratium furca occurred off Chicken Key from August through January being most abundant in December. Most of Davis's (1950) records for this species on the east coast of Florida are for the fall, although he also records it as being common in the vicinity of Key Largo in March, and Davis and Williams (1950) record it in the Florida Bay area in May and June. Johnson (1932) found *Ceratium furca* to be most numerous in the fall and early winter in Friday Harbor.

Graham and Bronikovsky (1944) state that *Ceratium furca* is a cosmopolitan species in oceanic regions, where it exhibits an *in situ* temperature range of 6.6° to 29.4° C and a salinity range of 33.1 to 37.0 $^0/_{00}$. Davis and Williams (1950) record this species in a salinity of 8.6 $^0/_{00}$ from Seven Palm Lakes in Southern Florida.

Ceratium macroceros (Ehrenberg)
Temperature Range: 15.6-30.0° C
Salinity Range: 14.8-25.1 $^0/_{00}$

Ceratium macroceros occurred from October to January and was the least abundant species of *Ceratium* encountered. Davis (1950) has records of this species throughout most of the year in the more open waters of the east coast of Florida.

In Friday Harbor *Ceratium macroceros* is also not abundant, but is most numerous in the fall and winter months (Johnson, 1932). Fish (1925) records this form at Woods Hole from August to January with maximum numbers in October.

Of the two subspecies of *Ceratium macroceros* listed by Graham and Bronikovsky (1944) for the North Atlantic, *C. m. gallicum* is apparently the one occurring in the Miami area. For this subspecies they record a temperature range of —1.6° to 29.4° C and a salinity range of 31.7 to 37.1 $^0/_{00}$.

Lucifer faxoni Borradaille
Temperature Range: 20.5-27.9° C
Salinity Range: 19.3-34.2 $^0/_{00}$

Lucifer faxoni occurred rather regularly from mid-October through mid-February and appeared once in April (See Table II). Early in December a female carrying eggs was encountered in water with a temperature of 22.2° C and a salinity of 23.0 $^0/_{00}$. However, it appears doubtful that *Lucifer faxoni* completes its life history in the western part of Biscayne Bay since the zoea and mysis stages of this sergestid were never encountered at Chicken Key. The absence of the larval forms suggests that they are unable to survive in these inshore waters. It would accordingly appear that *Lucifer faxoni* is not endemic in the Chicken Key area, but that the adults drift inshore from more open waters. Davis (1950) discusses an unidentified species of *Lucifer* which is largely confined to the more open waters of the Miami area and is probably identical to *Lucifer faxoni*. Deevey (1952a, 1952b) records *Lucifer faxoni* from Block Island Sound from August through October.

Mnemiopsis mccradyi Mayer
Temperature Range: 24.3-27.9° C.
Salinity Range: 19.8-30.9 $^0/_{00}$

The seasonal distribution of this large ctenophore is shown in Figure 3. The possible effect of this species on the zooplankton in general has been discussed.

Additional forms

Pelecypod veligers occurred regularly throughout the year, but were more prominent from August through October. Echinoplutei occurred irregularly throughout the year but were most abundant in August. Various types of hydromedusae occurred regularly throughout the year, but achieved importance in the plankton only in July and August. Among the other plankters recorded, the more important forms were barnacle nauplii and cyprids, larvaceans, larval polychaets, and fish eggs.

Discussion

Comparison to the Seasonal Zooplankton Cycle in the Temperate Region

The seasonal distribution of the zooplankton in various coastal waters of New England has been presented by Deevey (1948, 1952a, 1952b, 1956), Riley (1941) and Riley and Conover (1956). Of these presentations that of Riley and Conover for four inshore stations in Long Island Sound seems to offer the best basis for comparison to the present study because of the nearshore location, average salinity and methods employed. Deevey (1956) also presents data for these four stations.

Riley and Conover average zooplankton volumes from all four stations to show for 1952 a well-defined maximum from mid-August through September and more poorly-defined and more brief maxima in March and May. For 1953 these authors show no well-defined maxima, but find the plankton volume most concentrated from August through October with a brief maximum in April. In an earlier study involving collections from inshore localities in Long Island Sound, Riley (1941) found a well-defined zooplankton maximum in September of 1938 and August of 1939.

The occurrence of well-defined maxima in August and September in the nearshore waters of Long Island Sound is similar to the situation in Biscayne Bay where the maximum occurred in October. The most pronounced dissimilarity between the two seasonal cycles results from the absence of a spring maximum in Biscayne Bay, whereas such a maximum is usually present in Long Island Sound. Another dissimilarity which occurs is the very brief mid-winter reduction in standing crop in Biscayne Bay in contrast to a mid-winter minimum of several months' duration in Long Island Sound. The virtual absence of a mid-winter reduction in zooplankton in Biscayne Bay may be attributed to the higher water temperatures. The average surface water temperature for December, January and February in Biscayne Bay is 23.3° C. For the same period at inshore localities in Long Island Sound, the average surface water temperature is about 3° or 4° C (Riley, 1941; Riley, 1956). Temperatures comparable to the mid-winter temperatures in Biscayne Bay occur in Long Island Sound only in the mid and late summer months. The higher winter water temperatures may also explain the absence of a spring zooplankton maximum in Biscayne Bay. It seems logical that phytoplankton and zooplankton production might continue more or less unabated through the winter in Biscayne Bay, thereby preventing an accumulation of nutrients and consequent phytoplankton and zooplankton spring maxima.

The single point of similarity between the zooplankton cycles in Biscayne Bay and Long Island Sound is the pronounced fall maximum. However, statistical analyses indicate that the ecological factors producing the fall maxima in the two localities are different. Correlation coefficients to illustrate the degree of relationship of temperature, salinity and rainfall to the weekly plankton volumes taken at Chicken Key are shown in Table III. Correlations above 0.29 are statistically significant at the 5 percent level of probability.

Table III. Correlation coefficients of plankton volume with rainfall, salinity and temperature at various time lags. Coefficients shown in parentheses have been calculated omitting the three weeks of the October plankton maximum.

Time Lag	Rainfall	Salinity	Temperature
Same week.......	.23	−.48(−.10)	.05(−.23)
Previous week....	.61	−.34	
2 weeks previous..	.69(.06)		
3 weeks previous..	.39		

Riley (1941) states that in Long Island Sound the "zooplankton shows a significant correlation only with temperature, which appears to be the most important, if not the only, controlling factor." In Long Island Sound August is the month of highest surface water temperature as well as the month of the zooplankton maximum. In Biscayne Bay, however, no very significant correlation between zooplankton and temperature was found. At the Chicken Key Station near-maximum surface water temperatures prevailed for a four-month period from June through September with the zooplankton maximum occurring early in October when the average water temperature had declined only slightly. From July through September the zooplankton volume was at its lowest value. For the entire year of 1948 the correlation coefficient of 0.05 indicates no linear relationship between zooplankton volume and temperature.

The lack of significant linear correlation between zooplankton and temperature found here is in agreement with the conditions encountered by Deevey (1948) in Tisbury Great Pond, where the correlation coefficient for the same two variables was found to be "close to zero."

Cause of the October Maximum

There are apparently only two established causes of zooplankton maxima. These are an increase in the quantity of phytoplankton when it is the limiting factor and an increase in temperature when it is the limiting factor. The occurrence of the former phenomenon has been recorded off Plymouth by Harvey (1934) and Harvey, Cooper, Lebour, and Russell (1935) and on Georges Bank by Riley and Bumpus (1946). This is regarded as a general phenomenon by Riley, Stommel and Bumpus (1949). The occurrence of the latter phenomenon has been recorded in Long Island Sound by Riley (1941) and in the Gulf of Maine and the Bay of Fundy by Fish and Johnson (1937).

Since, on the basis of the correlation coefficients, temperature does not appear to be the factor limiting zooplankton production off Chicken Key, it is probable that phytoplankton is the limiting factor and, therefore, that an increase in phytoplankton preceded the zooplankton maximum. The hypothesis that phytoplankton is the factor limiting zooplankton production is supported by Smith *et al.* (1950), who refer to "generally low phytoplankton volumes" and "grazing rate limited by phytoplankton formation" in Biscayne Bay. Moreover, in the Tortugas region, Riley (1941) has shown that phytoplankton production and the phytoplankton standing crop as well as the quantity of chlorophyll per animal are definitely low, at least when compared to Long Island Sound. A phytoplankton bloom occurring just prior to the October zooplankton maximum could have been missed in the interval of a week or may well have gone unsampled since phytoplankters in general are too small to be retained by a Number 6 net. In the Tortugas region Riley (1938) found that a Number 20 plankton net retained less than 2 percent of the phytoplankton as determined by the total plant pigments method.

The October zooplankton maximum was made up primarily of the copepod *Acartia tonsa* with individuals of this species being particularly numerous at the beginning of the maximum (Figure 4). It has been suggested above that *Acartia tonsa* spawns throughout the year in Biscayne Bay. It is also entirely possible that a low phytoplankton production, which has been postulated above for Biscayne Bay, normally results in a heavy mortality of the nauplii of this copepod as well as of the larval stages of other zooplankters. In this connection Marshall, Nicholls and Orr (1934) have found that a spawning of *Calanus finmarchicus* may be "abortive owing to scarcity of food for the early stages of development." If it were true that the production of *Acartia tonsa* is normally limited by the phytoplankton production, the total quantity of copepodids and adults of this species would remain fairly low throughout the year despite continual spawning. If, then, a major phytoplankton bloom should occur, the *Acartia* nauplii should grow and mature rapidly with a much reduced mortality, producing a maximum initially composed largely of copepodids when sampled with a Number 6 net, which is too coarse to retain nauplii.

The *Acartia* collected during the first week of the October maximum were of a richer brown color than usual and after preservation showed large oil droplets within their bodies. The latter observation suggests a storage of fat. Marshall *et al.* (1934) state that in *Calanus finmarchicus* there are indications that a storage of fat can take place during periods of plentiful phytoplankton.

Although the data are not conclusive on this point, the most logical cause of the zooplankton maximum seems to be an unobserved phytoplankton bloom, which permitted greatly increased production of a zooplankton community which is normally limited by a low phytoplankton production.

Smith *et al.* (1950) suggest that in the Miami area land drainage is of great importance in the growth of plankton, presumably by the addition of nutrient salts to the water, although they state that this influence is apparently ineffective on the mangrove-fringed shores of the mainland. Presumably, then, land drainage should be unimportant to plankton growth at the Chicken Key Station. Smith *et al.* (1950) further suggest that plankton growth is limited the year around by the rate of phosphate production and that the grazing rate or rate of zooplankton production is limited by phytoplankton formation.

Assuming that land drainage is proportional to rainfall, a crude test of the validity of these suggestions as they might apply to the Chicken Key area of Biscayne Bay may be made by determining the degree of linear correlation which exists between the zooplankton volume and rainfall as measured at nearby Chapman Field.

By correlating plankton volume with the rainfall for a seven-day period immediately preceding the collection of plankton and with the rainfall for successively earlier seven-day periods, one finds the highest correlation with the rainfall of a seven-day period which ended two weeks before the collection of the plankton sample (See Table III). However, where a correlation coefficient is determined with the same time lag but without using the three points representing the October maximum of plankton volume, and the corresponding weekly rainfalls, the coefficient drops to 0.06. It is accordingly apparent that the value of 0.69 is due almost exclusively to the values for the three-week period of the October maximum and that there is no significant linear correlation between plankton volume and rainfall for the other forty-nine weeks of the year. One may conclude, therefore, that rainfall and consequent land drainage into Biscayne Bay have no effect upon the volume of the zooplankton community at the Chicken Key area with the possible exception of the very heavy rainfall of the latter part of September which preceded the October plankton maximum by two or three weeks.

Whether or not this very heavy rainfall and consequent land drainage added nutrient salts to the Bay, permitting a phytoplankton bloom and the subsequent October zooplankton maximum, cannot be positively stated. It is only the most likely explanation afforded by the data at hand. Other explanations are possible. The winds of hurricane velocity which moved through the Miami area on September 22, 1948, might have effected a renewal of nutrients to the surface waters, where they could be utilized by the phytoplankton.

If the heavy rainfalls of the latter part of September and consequent land drainage or the hurricane winds did effect an addition of nutrient salts to the waters of Biscayne Bay, permitting thereby a phytoplankton bloom which would make possible the October zooplankton maximum, these events must have occurred in a period of about two weeks. Since the water temperature for a two-week period immediately preceding the October maximum averaged 29.0° C, the biological processes could have occurred rapidly. Moreover, the proper timing of a phytoplankton bloom with the appearance of a new brood of *Acartia* nauplii as well as of the brachyuran zoeae which contributed to the maximum could have rapidly brought about a zooplankton maximum. In this connection Marshall *et al.* (1934) and Clarke (1939) have commented on the importance of the timing of phytoplankton blooms with the appearance of new broods of copepods.

The correlation between zooplankton volume and salinity is negative and significant, though not as marked as the rainfall correlation for the entire year. However, when the three weeks of the October zooplankton maximum are omitted from the calculation of the correlation coefficient, it drops to an insignificant —0.10. Accordingly, the correlation coefficient of —0.48 is due very largely to the low salinities which occurred during the October zooplankton maximum. These low salinities are not construed as a causative agent of the October zooplankton maximum, but are looked upon as a result of the heavy rainfalls which preceded the maximum by two or three weeks.

Deevey (1948) found no correlation between total zooplankton quantity and salinity.

SUMMARY

A series of zooplankton samples was taken at weekly intervals from November, 1947, to December, 1948, in Biscayne Bay off Chicken Key. The seasonal cycle of the zooplankton was compared to the water temperature, salinity and local rainfall. The seasonal distribution of the volume of the entire community sampled showed a sustained summer minimum followed by a brief but well-defined maximum in October. The October maximum as well as most of the other plankton volume peaks was composed largely of the copepodids of *Acartia tonsa*.

The plankton community was composed predominantly of gastropod veligers, copepods and decapod zoeae. Only the copepod population has been considered in detail. An examination of the seasonal variation in the sex ratio of *Acartia tonsa* has led to the suggestion that this calanoid produces about eleven generations per year and that the time interval between successive generations varies from 4 to 7 weeks depending on the temperature. Although *Acartia tonsa* is certainly the dominant copepod off Chicken Key a considerable portion of the *Acartia tonsa* population is replaced in the winter and spring months by *Paracalanus parvus*. Correlation analyses suggest that temperature is the factor controlling the relative numbers of these two copepods.

In addition to *Acartia tonsa* and *Paracalanus parvus,* the copepods that occurred throughout the year off Chicken Key are *Oithonina nana,* which showed a mid-winter maximum and *Metis jousseaumei,* which showed a mid-summer maximum. Two species of *Labidocera* occurred through most of the year, but *L. scotti* was absent during the mid-summer months and *L. mirabilis* was absent during the late summer and early fall. *Acartia spinata* occurred only during the summer, but then in some numbers. *Pseudodiaptomus coronatus* oc-

curred only during the late fall and early winter months. *Temora turbinata, Euterpina acutifrons* and *Monstrilla floridana* occurred only during the winter months. *Calanopia americana* occurred during the winter and spring, and *Monstrilla reticulata* occurred in the winter, spring and summer.

A comparison of the seasonal distributions in Biscayne Bay to those in New England waters suggests that the prevailing temperature does not influence the seasonal distribution of *Acartia tonsa* and *Pseudodiaptomus coronatus,* but does influence the seasonal distribution of *Paracalanus parvus.*

The three species of *Ceratium* encountered are fall and early winter forms, with *C. fusus* being most abundant in October, *C. furca* being most abundant in December, and *C. macroceros* showing no maximum.

The decapod *Lucifer faxoni* occurred during the late fall and winter months, and the ctenophore *Mnemiopsis mccradyi* occurred in the late fall and early spring.

The seasonal plankton cycle found in Biscayne Bay is compared to similar cycles found at more northern latitudes along the east coast of the United States. The probable cause of the October zooplankton maximum is discussed.

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MAMMALIAN SUCCESSION ON MIDWESTERN FLOODPLAINS[1]

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Although certain changes in mammalian species with changes in land and plant cover are frequently inferred, no studies of mammalian succession on midwestern floodplains were found in the literature. Smith Davidson (1928) mentioned mammals in her study of animal succession in Illinois, although her quantitative sampling was restricted to invertebrates. Smith (1940) included mammals in his study of old field succession in Oklahoma. Aldrich (1943) reported on mammals in his studies of succession in the swamp seres in Ohio. Verts (1957) sampled small mammals during seven months (representing summer, winter, and spring in that region) in strip-mined uplands in southern Illinois. As his series of sampling areas ranged from five to twenty-three years since having been strip-mined, he examined his results in terms of population (two species of *Peromyscus*) and plant cover change.

The present report is concerned with changes in mammalian species and populations in a deciduous forest sere starting from artificially cleared floodplains. The study was initiated in 1940-41 and intermittently followed between 1946 and 1955. Earlier reports and photographs of some of the strip-mine areas permit expansion of this period to nineteen years.

I am indebted to Dr. V. E. Shelford during 1940 and 1941 and to Dr. S. C. Kendeigh after 1946 for their helpful advice and guidance.

Description of Study Areas

The coal stripped lands used for the study are located along the Middle Fork and Salt Fork river bottoms, chiefly in Kickapoo State Park, six miles west of Danville, Illinois (Fig. 1). They present the usual appearance of stripped lands, with alternating ridges or spoil banks and valleys, interspersed with some ponds or small lakes. The heights of the spoil banks are generally lower than

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[1] Contribution from the Department of Zoology, University of Illinois, Champaign.

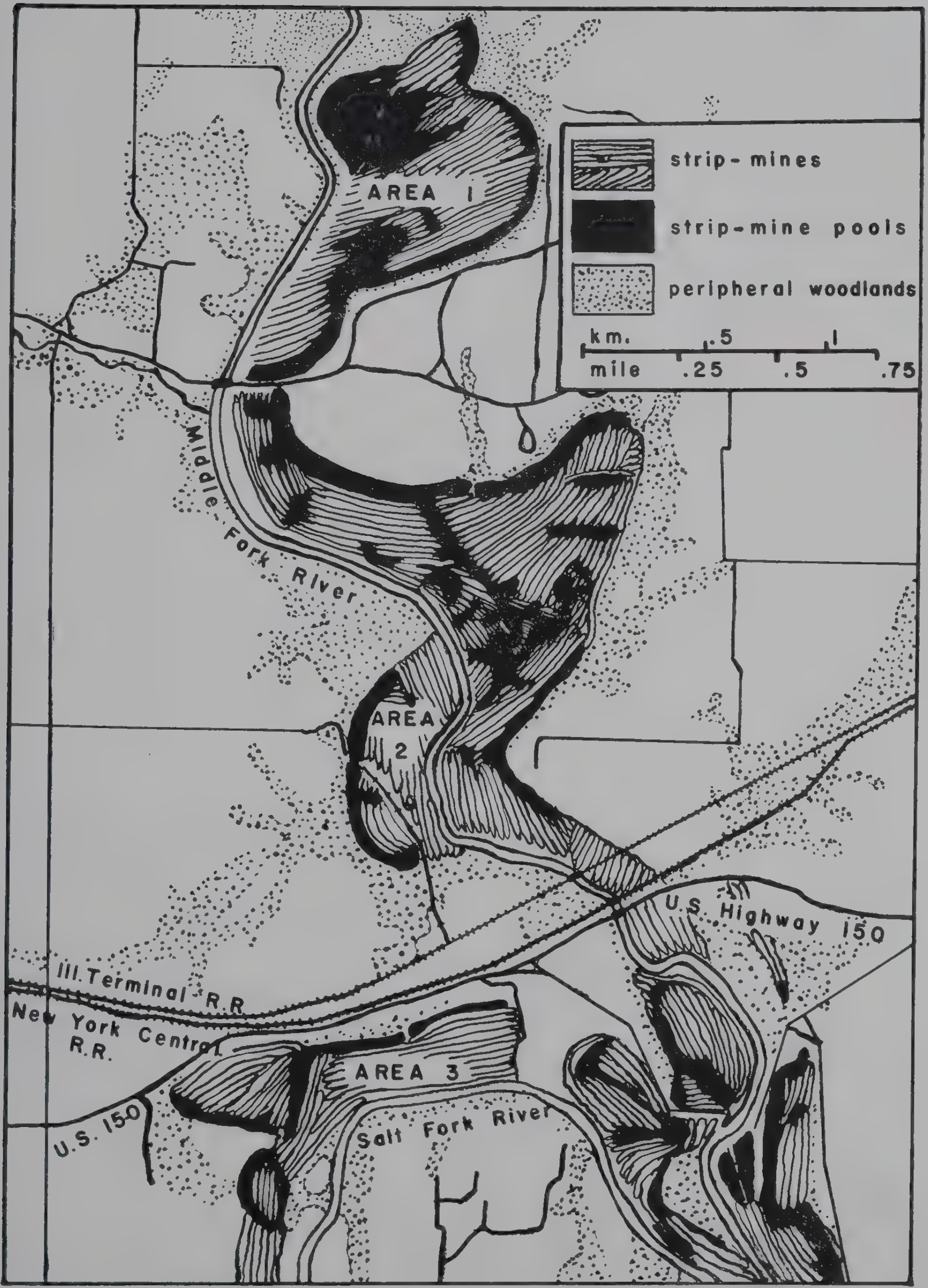
strip-mines
strip-mine pools
peripheral woodlands
km.
.5
1
mile
.25
.5
.75
AREA 1
AREA 2
AREA 3
Middle Fork River
Salt Fork River
U.S. Highway 150
U.S. 150
Ill. Terminal R.R.
New York Central R.R.

Fig. 1. Map of the strip-mines, based upon aerial photographs taken for the Illinois State Natural History Survey, 1939.

in newer strip-mines in part due to the increase in size of power shovels and also, perhaps, to lesser amounts of overlay to be removed.

The plant succession and physiographic features of these strip-mines have been described by McDougall (1918, 1925) and Croxton (1928). They differ from those reported by Bramble and Ashley (1955) in Pennsylvania and by Brewer and Triner (1956) and Verts (1957) in southern Illinois by having an initial herb-grass stage prior to the invasion of the majority of tree seedlings.

Invertebrate succession has been reported for these strip-mines by Smith Davidson (1928). Costley (1936), in addition to sampling for invertebrates and cruising for birds, based his reports of mammals upon signs, interrogation of fur trappers, and upon trap lines. Approximate (and in some cases, exact) determination of his areas was possible from his thesis and photographs. Yeager (1942) discussed the major plants and mammals on the area and emphasized the value of the strip-mines as wildlife habitat.

AREA 1 is approximately 30 acres (12 hectares) in size, being interspersed with ponds and irregularly confined by a tall levee bounding the present channel of the Middle Fork River on the west and lagoons and bluffs on its other boundaries. It had been strip-mined in 1933 and by 1936 had, at best, a very sparse plant cover (Figures 2, 3). Costley (1936) mentions white clover (*Trifolium repens*), sweet clover (*Melilotus alba*), *Aster,* and cockleburs (*Xanthium* sp.), although these cannot be detected in his photographs. By 1940 the plant growth had almost covered the area, with sweet clover, aster, and ragweed (*Ambrosia* spp.) predominating, leaving only the tops of the spoil banks bare (Figure 4). Only a few small tree seedlings (maximum height 3 feet, chiefly ash, *Fraxinus* sp.) and trumpet vines (*Campsis radicans*) could be found. Moss covered approximately one-fourth of the north sides of the spoil banks. Cattails (*Typha latifolia*) grew in the deeper hollows.

By 1946 the plant growth had covered the tops of the ridges. Some of the trees had reached a height of 11 feet. Colonies of trumpet vines were now evident features on the area. Moss covered an estimated one-half to three-quarters of the north sides of the spoil banks, under the annuals. The appearance of this area by 1949 was essentially the same except for an increase in the number and size of the trees, trumpet vines, and briars (Figure 5).

By 1955 (Figure 6) the appearance of this area was quite similar to that of Area 2 in 1940. The trees were generally those of the older areas and included box elder (*Acer negundo*), ash (*Fraxinus* sp.), soft maple (*Acer saccharinum*), elm (*Ulmus* spp.), cottonwood (*Populus deltoides*), willow (*Salix* spp.), and sycamore (*Platanus occidentalis*) at heights approximating twenty feet. As the canopy was open (less than forty per cent cover), the term forest edge is used for this stage in succession. Trumpet vines, sumac (*Rhus* sp.),

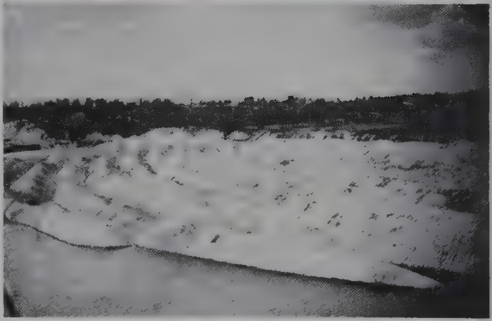

FIG. 2. Panorama of Area 1, three years after stripping. Small, isolated clumps of vegetation. (Photographed by R. J. Costley, 1936.)

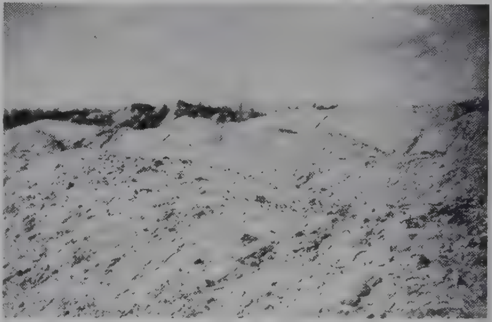

FIG. 3. Area 1, three years after stripping. (Photographed by R. J. Costley, 1936.)

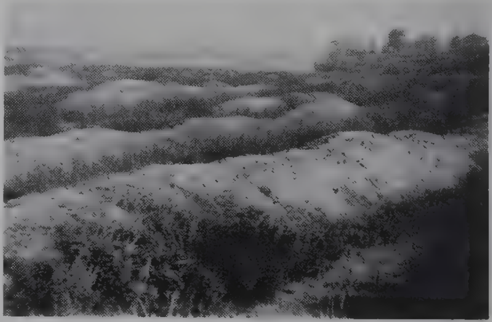

FIG. 4. Area 1, seven years after stripping, with annuals covering the sides of the spoil banks and some cattails in the valleys. (Photographed by writer, 1940.)

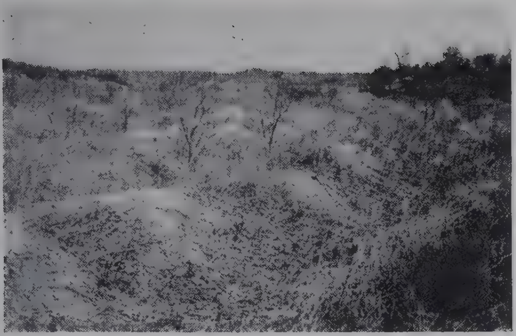

FIG. 5. Area 1, seventeen years after stripping, with vegetation completely covering the spoil banks and with some small trees present. (Photographed in the winter, 1949, by the writer.)

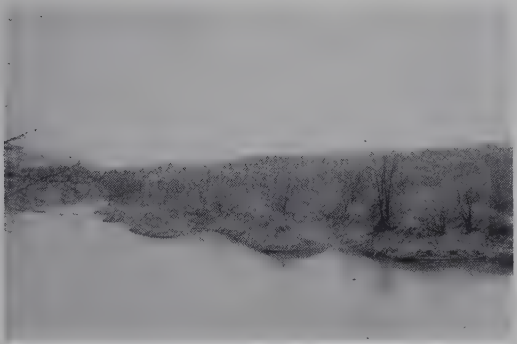

FIG. 6. Area 1, twenty-two years after stripping, with numerous trees, some of which are twenty feet in height. (Photographed by R. Brewer, 1955.)

briars (*Rubus* spp.) and grasses were evident throughout the area and, in places, quite dense.

AREA 2 is approximately 67 acres (27 hectares). It is confined between the present channel of the Middle Fork River and the bluffs marking the outside curve of the former channel. It is estimated that this area was stripped twenty-five to thirty-five years ago, on the basis of its appearance in 1936, as described and photographed by Costley. At that time there was complete plant coverage, chiefly clover and aster, with some rye grass (*Elymus* sp.) and tree seedlings.

By 1940 the ground cover was predominantly trumpet vine, sumac, briars, and grasses, in varying degrees of dominance in different locations. Elm, cottonwood, box elder, willow, ash, soft maple, and sycamore at heights of 10-20 feet were noted on the area (Figure 7). These trees were openly distributed, with only 6 on a half-acre trapping plot.

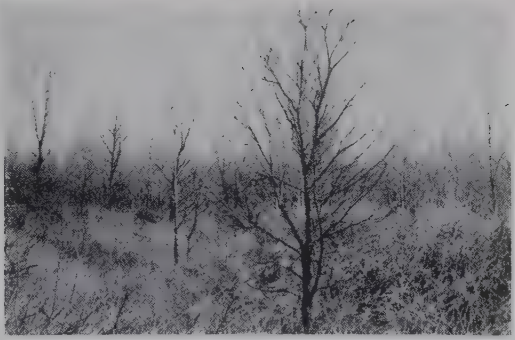

FIG. 7. Area 2, 1940. Note tangle of trumpet vines.

Changes in this area after 1940 include increase in size of the trees and reduction in sharpness of the spoil bank profiles. Although the forest canopy had increased by 1955, it was still essentially open.

AREA 3 is approximately 30 acres (12 hectares) in size. It is bounded on the south by the Salt Fork River and on the north by lagoons and bluffs. Its east and west margins are bounded by ecologically younger stripped areas. This oldest strip-mine was outside the limits of Kickapoo State Park, and the only one that was seasonally flooded. Spoil banks, the result of strip mining in the early part of this century, had been eroded and silted into relatively low rounded contours.

In spring and summer there is a high herb layer of wood nettles (*Laportea canadensis*) and jewel weed (*Impatiens* sp.). The vine growth is heavy and consists chiefly of poison ivy (*Rhus radicans*) and Virginia creeper (*Parthenocissus quinquefolia*). During the fall and winter months, however, the forest floor is open and bare areas of fresh silt are more noticeable. The tree canopy is nearly complete. These floodplain trees are soft maple, box elder, ash, elm, cottonwood, and sycamore.

SANGAMON RIVER FLOODPLAIN. This mature floodplain forest is located one mile northwest of White Heath, Piatt County, Illinois, and 40 miles west of the strip-mines. It has been described by Fawver (1947). Elm and soft maple are the dominant trees both here and in the ecologically younger strip-mine forest. In the older floodplain of the Sangamon cottonwood and sycamore are proportionately less in abundance and hackberry (*Celtis occidentalis*), yellow-bud hickory (*Carya cordiformis*), ironwood (*Ostrya virginiana*), and bur oak (*Quercus macrocarpa*) are additional components. Wood nettles are the most abundant herbs in both areas, while giant ragweeds (*Ambrosia trifida*) under breaks in the tree canopy are peculiar to the Sangamon. In both areas vines are abundant. The numerous fallen trees, stumps, and old hollow trees of the

Sangamon are largely lacking in the young floodplain of the strip-mines. So, although seasonal floods probably equally restricted the availability of ground home sites for mammals, refuges in the trees above flood level are much more evident in the Sangamon area.

BROWNFIELD WOODS. Although never flooded, this area has a small stream and floodplain. It could be considered a habitat for mammals comparable to the product of floodplain succession in this region. The woods is a 60-acre tract of continuous, climax oak-maple forest owned by the University of Illinois. It is located 5 miles northeast of Urbana and approximately 25 miles west of the strip-mines. As the tract is left in an undisturbed condition, hollow trees, fallen logs, brush from newly fallen trees, and a thick layer of humus and litter on the forest floor present numerous home sites for mammals.

Sampling Procedure

The small Sherman live-trap was used in the 1940-41 trapping, set at 24-foot grid intervals on measured plots in each of 3 areas in the strip-mines. Small wooden shelter boxes fitted on the ends of each trap were kept supplied with food and dry cotton waste. Because of the small size of the quadrats (½ acre in the fall of 1940 and 1½ acres in the spring of 1941) and the low numbers of mice that were trapped three or more times in other than the border traps, mean movement areas could not be calculated for use in population estimates. In estimating these populations, following the method used by Burt (1940), a 75-foot mean radius was used for the prairie deer mouse, *Peromyscus maniculatus bairdi*, (Blair, 1940) and 63-foot mean radius for the white footed mouse, *P. leucopus noveboracensis*, based on live-trapping studies in Brownfield Woods (Wetzel, 1949). Dry oatmeal and raisins were used for bait.

In 1946 lines of snap-traps were run for 28 trap-nights in each strip-mine area. Bait (nutmeats), trap interval, trap numbers, and days of trapping were kept constant in all cases.

Circular acre snap-trap plots were employed on the same areas in 1948 and 1955 and in Brownfield Woods in 1946 and 1948. The traps were set without pattern within the measured circle except with intent to trap all mice during a three day period. Nut meats were used as bait.

Nearly complete sampling of the entire strip-mine was afforded by exploratory trap-lines set well outside of the trapping plots. These lines, plus cruising for mammal signs, and collecting cans sunk in the ground supplemented the measured area trapping and permitted an increase in species coverage.

Dr. Ben. J. Fawver and the author live-trapped a 2.1-acre rectangular quadrat for five days in the Sangamon River floodplain in July, 1946, using 45-foot grid intervals. The area had been flooded one week prior to trapping.

Although trapping during this study totaled 6,502 trap-nights, the results are strictly comparable only between seasons and between the different areas for one season where only one trapping method was used. The results are not presented in trap-nights because of the vast difference in the number of animal movement areas traversed by the trapping patterns of the plots versus trap-lines or differences in concentration of traps and plot size between snap-trap plots and live-trap quadrats. The results from the trap-lines are thus comparable only qualitatively with the results from live- and snap-trapping. The validity of comparing results from snap- and live-trapping quantitative methods has been seriously questioned by Stickel (1946a, 1946b). For the purposes of this present report estimates based upon these two methods are considered comparable at the low population levels found in the strip-mines, as suggested by five separate comparisons made by the author (Wetzel, 1949) following Stickel's methods.

Results and Discussion

Table I is a summary of only the standardized collections made during this study. From these data a schematic picture of small mammal succession as correlated with plant succession has been made against a chronological scale and this is shown in Figure 8.

The mammals which were found to display a successional pattern are discussed in approximate order of their succession. The omissions consist of the larger mammals, many of which are aquatic, whose extensive ranges carry them into all of the habitat types. For example, muskrat (*Ondatra zibethica zibethica*) left tracks in all of the strip-mine series. With numerous ponds and waterways throughout the area its establishment is dependent only on the development of sufficient aquatic food (mussels) and water edge food (cattails, white clover, wild parsnips, *etc.*). The latter food group was present in less than ten years after stripping. Mussel shells were observed along the margin of the water near Area 1 in 1946.

Peromyscus maniculatus bairdi (Hoy and Kennicott). One of the earliest invaders, the prairie deer mouse, was found at a density of nine per acre in October, 1940, four to six years after

TABLE I. Occurrence of certain mammals in deciduous forest succession. Figures represent estimates per acre unless indicated as follows: ( ) catch in traplines of standard length for 28 trap nights; B catch in bucket traps; X supplementary traplines

		AREA 1, STRIP-MINES (annuals to forest-edge)				AREA 2, STRIP-MINES (forest—grass, briars, trees)			AREA 3, STRIP-MINES (young floodplain forest)				MATURE FLOOD-PLAIN FOREST, SANGAMON RIVER	CLIMAX OAK-MAPLE FOREST, BROWNFIELD		
	Season	Mar. April	May June	Aug.	Oct. Nov.	Mar. April	Aug.	Oct. Nov.	Mar. April	May June	Aug.	Oct. Nov.	July	May June	Aug.	Sept
prairie deer-mouse	1941-40	4	13		11	..		..	.			.				
	1946		(3)		(12)			..				..	.	..	.	.
	1948	8			6	..		..	..			..			..	
prairie vole	1946		(1)		..			(2)				.	.	.	.	.
	1948	1			..			..							.	.
	1955			7			.				..					
house mouse	1941-40	1	..		2	1		..	..			.				
	1946		..		..			..				..	..	..	1	1
	1948	..			..	..		1		..					..	1
large short-tailed shrew	1946		(1)		..			..				..	X	1	1	1
	1948	..			..	..		2				X			7	3
	1955		..				4				2					
bog lemming	1946		..		..			2				..	..	.	..	
	1949-48	..	..		..	B	..	..	.	..	..	..			..	.
grassland jumping mouse	1941	..	..		..	1		..	..			..				
	1949-48	..	..		..	B	..	..	.	..	..	..				
woodland white-footed mouse	1941-40	..	..	..	..	..		..	2	.		3				
	1946		..		..			..			.	(3)	24	11	18	24
	1948	..			..	..		1		8					11	15
	1955		.	7			4		.		1					

stripping operations had ceased. The invasion onto stripped lands probably occurs from sodded roadside and mine railway grass strips that penetrate the strip-mines.

Before stripping operations occurred, this land was in floodplain forest, a habitat in which *P. m. bairdi* is not found. This species is shortly succeeded by the woodland deer mouse, *P. leucopus noveboracensis*. As no *P. maniculatus* were collected in Area 1 by 1955 and in repeated trappings of Area 2 and surrounding land, it is believed that by the time the invading trees have developed to about twenty feet in height (as was Area 2 in 1940 and Area 1 in 1955), twenty years' (plus) development from bare strippings, the prairie deer mouse has dropped out of the mammalian succession. This could be due to a psychological preference for a treeless habitat (Harris, 1952).

No climatic or physiological differences have been found that would explain its obvious choice of a grassland habitat (Dice, 1922; Johnson, 1926). Although many of the types of seeds stored by *P. m. bairdi* (Allen, 1938; Howard, 1949) are available to this species only in that portion of strip-mine succession in which it is found, Cogshall (1928) concluded from food preference experiments that food is not an important factor in limiting habitat distribution in this and other species of deer mice.

The den holes of these mice were in the sides of the spoil banks in the stands of vegetation but sufficiently above the valleys to avoid the intermittent flooding. However, the mice ranged freely over both the bare tops of the spoil banks and the vegetation-clogged valleys during the hours of dusk and darkness. The total daily catch of *P. m. bairdi* in 112 traps on ridges was 59, and the total daily catch in 92 traps in valleys was 50 (from live-trapping data, 1940-41, Area 1).

Microtus ochrogaster ochrogaster (Wagner). The prairie vole (yellow-bellied meadow mouse) was conspicuously absent from Area 1 in 1940-41, although collected there by 1946, thirteen years after stripping. Optimum conditions were found in the homogeneous grass patches, near Area 2. This is in keeping with its food preference for roots and stems of grass (Schmidt, 1931; Fisher, 1945; Jameson, 1947; Martin, 1956) as well as its tunneling habits in grass. The trumpet vine

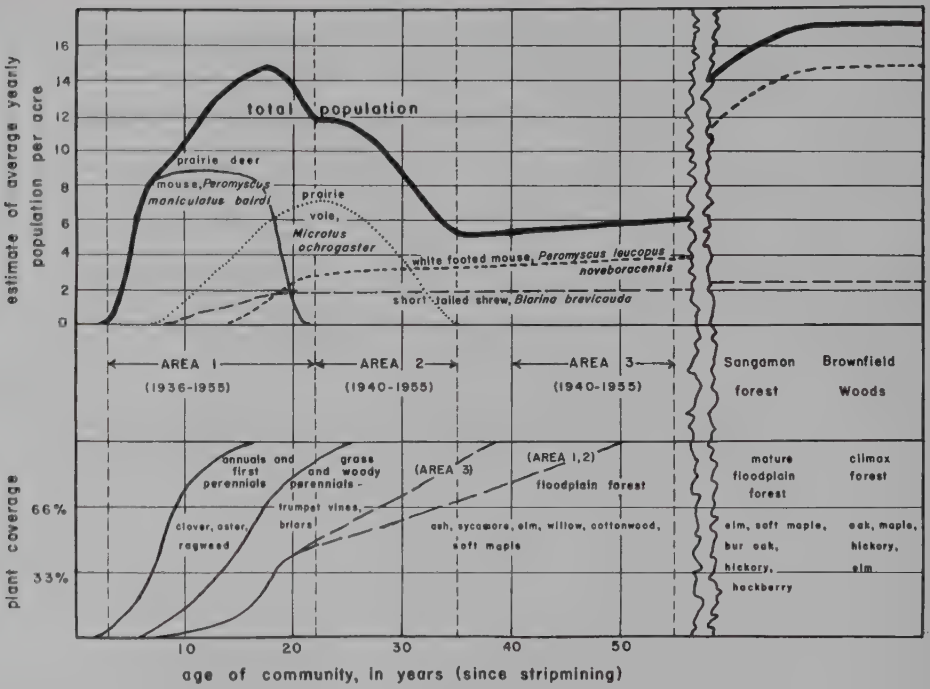

FIG. 8. Succession of small mammals and their habitats. Average population figures are based, where possible, upon the means of fall (high) and spring (low) population estimates.

tangles of the same stage supported a very low population.

The eastern meadow mouse, *M. pennsylvanicus pennsylvanicus* has been reported as probably occurring in these strip-mines by Costley (1936) and Yeager (1942). The specimens responsible for these reports are actually bog lemming, *Synaptomys cooperi* (Wetzel, 1947).

Mus musculus Linnaeus. The house mouse was trapped occasionally in Areas 1 and 2. No evidence was obtained that it breeds in the strip-mines. It probably invades nearly all areas of the mines but is rarely successful in establishing a permanent population.

Blarina brevicauda (Say). The large short-tailed shrew invades the stripped areas when the sweet clover-aster-ragweed stage is reached but does not succeed in establishing a population recordable throughout the year until the briar-grass-trumpet vine-tree stage. Highest populations occurred on the grassier sites of the latter stage. In the older, forested stage, *Blarina*, with the woodland deer mouse, *Peromyscus leucopus*, constituted the major elements of the small mammal population.

Blarina was noticeably restricted to habitats permitting burrowing as well as those shown by Smith Davidson (1928) as having larger numbers of invertebrates. This habitat selection can perhaps be explained by a combination of its requirements: (1) Physiologically it is restricted to a relatively moist habitat with runways and tunnels in either grass or forest floor and by a water turnover rate found by Chew (1951) to be nearly twice that of *Peromyscus leucopus*. (2) It is largely dependent upon soil and litter invertebrates for food, as has been found from stomach analyses by Hamilton (1930, 1941), Schmidt (1931) and Calhoun (1941). This dependence is accentuated by the large amounts of food that it eats, a factor of its high metabolic rate (Pearson, 1947).

Synaptomys cooperi gossi (Coues). The southern bog lemming was collected only in the homogeneous grass patches mentioned above. Although it is only intermittently detectable, this species must be considered a typical member of the mammal population in the grassy patches in the vine-briar-tree stage. As grass is its predominant food (Howell, 1927; Burt, 1928; Stegman, 1930; and Hamilton, 1941), and as it is a shallow tunneling form, it invades the stripped lands only when sufficient grass sod has developed. It drops out of strip-mine succession after the tree growth, accompanied by forest floor cover, supplants the open grassy parkland stands.

Zapus hudsonius hudsonius Zimmerman. Because of its low numbers, the meadow jumping mouse is incidental in mammal succession. It was collected in Area 2 in 1941 and 1949. Its food preference for grass and sedge seeds (Schmidt, 1931; Sheldon, 1934; Quimby, 1951) is in keeping with its place in this sere.

Cryptotis parva (Say). The small short-tailed shrew was collected in large numbers in Area 1 in 1955.

Peromyscus leucopus noveboracensis (Fischer). The white footed mouse was trapped in Area 3, in low numbers in Area 2, and, by 1955, in Area 1. It was most abundant in the Sangamon floodplain and Brownfield Woods. This species becomes established in large areas some twenty years after the land has been stripped. At this stage of succession the habitat is no longer suitable for *P. m. bairdi,* nor is it optimum for *P. l. noveboracensis.* Because of low populations of the latter and the absence of the former at this stage, interspecific competition for food, den-sites, and home ranges are not considered important factors in the differential occurrence of these two species. Howard (1949) captured both *P. m. bairdi* and *P. l. noveboracensis* in the same nest-boxes, which would indicate no particular interspecific animosity. Food preference is not believed to be a prime factor in this habitat selection (Cogshall, 1928). No climatic differences between prairie and forest have been demonstrated to explain its habitat preference for forest and forest-edge situations (Dice, 1922; Johnson, 1926). A less tangible factor such as psychological preference for habitats with trees coupled with or caused by greater climbing ability (Horner, 1954; Harris, 1952) seems nearer the answer.

The increase in population of this species from the young floodplain of the strip-mines to the mature floodplain forest of the Sangamon and Brownfield Woods is striking. Correlated with this increase are increases in food (particularly acorns), home-sites, and refuges from flooding. The large population of deer mice in the Sangamon floodplain within a week after flooding indicates that refuge was obtained near at hand, probably in the trees. The presence of dens in trees and food in such refuges would play a large part in the maintenance of life during prolonged floods. Thus, the accumulation of tall stumps and large old trees with holes, as the floodplain community increases in age, is a trend toward better protection from flooding.

Scalopus aquaticus machrinus (Rafinesque). The youngest ecological stage at which mole tunneling was observed was the grassy briar-patches near Area 2. Tunneling was not common, however, until the heavily forested stage (Area 3). Because of its tunneling habits and dependence upon soil invertebrates for food (Dyche, 1903; Scheffer, 1910; West, 1910; Schmidt, 1931; Calhoun, 1941) and high food requirements (Hisaw, 1923), this mammal cannot successfully invade from heavy grassy sods and floodplain forests until a humus layer has accumulated. In both the strip-mines and the Sangamon floodplain fresh mole workings were commonly seen within a week after the areas had been flooded.

Sylvilagus floridanus mearnsi Allen. From sight records and observance of scat while trapping small mammals, it was noted that the heaviest population of cottontail rabbits was in the vine-briar-grass tree stage, although they were observed in all stages of the strip-mine sere.

Marmota monax monax (Linnaeus). From the location of burrows and sight records, it appears that the woodchuck invades the strip-mines from surrounding roadsides and exposed hillsides by the time the clover-aster stage is reached. The highest populations are reached in the vine-grass-briar-tree stage and the animals are present in the forested stage in reduced numbers only in sites along higher spillbanks where the tree canopy is not closed.

Citellus tridecemlineatus tridecemlineatus (Mitchill), the thirteen-lined ground squirrel, and *Citellus franklini* (Sabine) were not seen at any location within the strip-mines themselves. A number of small holes of likely sizes for both of these species were probed and found to end a foot or less from the surface. It appeared that some animals had evidently stopped their excavation upon reaching the hard packed pieces of shale and other rock. It is probable that these two species seasonally invade the stripped areas in the sweet clover to vine-briar-grass-tree stage from surrounding roads and old rail strips.

Sciurus niger rufiventer (Geoffroy). The fox squirrel invaded stripped areas from nearby forested hillsides when the tree development had progressed to a point now displayed in Area 2. However the community development reaches a stage more favorable for this species in the older forest, Area 3.

The chipmunk, *Tamias striatus griseus* Mearns, the gray squirrel, *Sciurus carolinensis* Gmelin, and the flying squirrel, *Glaucomys volans volans* (Linnaeus), were not observed in the strip-mines, although other records indicate their presence in some portions of the older strip-mines as well as in Sangamon and Brownfield Woods.

SUMMARY AND CONCLUSIONS

Mammal population changes were followed for fifteen years in a coal stripped floodplain in eastern Illinois. Three areas, strip-mined in 1933, 1920-30, and in the early part of this century were utilized for sampling and comparison. A mature floodplain forest and a climax oak-maple forest provided indications of the ultimate population in this succession.

The population level of small mammals in the strip-mine sere was quickly built up (well within a period of seven years from the time of strip mining operations, in one instance) entirely by the prairie deer mouse, *Peromyscus maniculatus bairdi*. Subsequent drop in numbers of these initial invaders was compensated by the invasion of the prairie vole, *Microtus ochrogaster,* the short-tailed shrew, *Blarina brevicauda,* and the white footed mouse, *Peromyscus leucopus noveboracensis*. The total small mammal population dropped as this forest edge stage (grass, briars, trumpet vines, and trees) was reached, except for probable (but unrecorded) fluctuations in the year to year microtine population. Typical grassland inhabitants of this forest edge stage such as *Microtus,* bog lemming, *Synaptomys cooperi,* and meadow jumping mouse, *Zapus hudsonius,* decreased in numbers as tree leaf litter and forest floor plants were exchanged for grasses. The development of the *Peromyscus leucopus* populations was very slow and did not compensate for the decrease in grassland forms. This was apparently correlated with the forty years required to develop a closed canopy (and resultant forest floor aspect) and the much longer time required for an accumulation of fallen logs, stumps, hollow trees, and the invasion of nut-bearing trees.

Differences between the strip-mine floodplain forest and the older forests studied were considered in the light of the higher populations of small mammals in the latter areas. Increasingly better surface drainage in the intervals between flooding may be expected as the ground level of the floodplain is raised by silting and by yearly accumulation of humus, and through lowering of the stream channels by erosion. Drier soil presents better conditions for tunneling and burrowing by small mammals and more nearly optimum habitats for invertebrate food. As the ground level rises increased protection from flooding will be afforded the small mammals and invertebrates. Thus, the trend toward a drier environment, the increase in old trees and potential home sites and refuges from floods, the increase in invertebrate food, and the increase in plant food resulting from invasion of tree species such as oaks and hickories all are trends in habitat succession which will permit an increase in the small mammal population.

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INTER-COMMUNITY RELATIONSHIPS IN HEMPHILLIAN (MID-PLIOCENE) MAMMALS[1]

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INTRODUCTION

The study of inter-community relationships in fossil mammals is a first step to the understanding of community dynamics involving geologic time. The lack of an effective method for delimiting communities in fossil mammals has long delayed the study of their community dynamics. The author (1955) has described and demonstrated an ap-approach which may be the needed tool.

The present study applies this method to data from a series of faunules of equivalent age. Limits and values of various sizes and kinds of samples to be used are examined.

METHOD

The basic purpose of the approach applied here is to distinguish from a quarry sample the mammals which live together in a community from those also appearing in the site but representing other communities. This separation is acccomplished by comparison of the relative completeness of various species represented, not by morphological characteritsics. Study of functional mor-

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[1] A number of individuals have helped in the course of the work described here. I wish to express my appreciation to my wife, Genevieve, and students, Huntley Alvey and Dale Russell for assistance in the field, to Messrs. Frank Swaggart, Walter Hamm, Kelly Tiller, Frank Swayze and Bill Belt of Hermiston, Oregon, for bringing the Westend Blowout site to our attention and aiding in the work there. We are grateful to Mr. Grattan L. Hoffmann of Boardman, for allowing us to make use of his collection from the Boardman locality.

This study was initiated with funds of the Research Committee of the University of Oregon, continued with funds of the American Philosophical Society and completed through support of the National Science Foundation.

phology of those mammals found to belong to the same community leads to an estimation of the probable type of habitat occupied by the community. These are two separate steps in this approach. The quantitative data collected from a quarry are analyzed applying the assumptions listed below.

1. Reasonably large collections from quarry accumulations are a random sample of what is present in the quarry providing all specimens are retained from the volume of sediment worked.
2. An indication of the relative density of mammals of the proximal community may be obtained from the use of the minimum number of individuals.
3. If a community other than the proximal one is represented in a quarry sample, the habitat of that community must be present in the region of the quarry.
4. Mammals whose community in life was close to the site of deposition will be more completely represented than will those whose community was farther away.

In the sites where this method has been applied there was little or no association of skeletal elements of any given individual. Materials collected were the separate elements of various animals. Each of these isolated skeletal elements is regarded as a specimen. The use of specimen to indicate an entire individual as used by zoologists is not possible under the conditions of occurence. The number of individuals of any particular mammal species represented in the materials from a site is not directly determinable. In order to find the relative abundance of species it is necessary to use the minimum number. The minimum number is that number of individuals which are necessary to account for all of the skeletal elements (specimens) of a particular species found in the site. This must be determined for each species. The relative completeness of various species is based on the ratio of the number of specimens per individual. Because of the variation in number of skeletal elements in different kinds of mammals the number of specimens must be corrected for each species. To do this the number is weighed against an estimated number of elements, the number less vertebrae and ribs which would be expected if all elements of the skeleton that can be recognized were recovered. The ratio of the corrected number of specimens per individual is the completeness of representation of the mammal in the sample. The mammals which belong together in a community are distinguished from those of other communities by their greater relative completeness. The community of the mammals with the greater relative completeness is the one nearest to the site of deposition and is therefore referred to as the proximal community. The majority of the mammal material collected at a site will belong to this community. The relative completeness and the relative abundance are indicated on a faunal analysis diagram, several of which appear later.

This brief résumé is meant only to re-acquaint the reader with the method and not to form a basis for understanding it. A complete description is presented in the article previously referred to.

In the following discussion the use of *faunule* is meant to imply that a sample represents a particular aspect of the entire fauna of a region, not a suggestion of size of the sample. The *fauna* is the whole of these aspects or faunules of a given area and time. The term *regional community* is used to indicate the community of the fauna. When intercommunity relationships are discussed they are described under the term *regional community organization.* These may not be proper in strict usage, but no really adequate terms are established. These are close enough in their usual application to be used here, avoiding the coining of new terms.

Estimated Number of Elements

Discussion with other works has led the author to feel that a standardization of the estimated number of elements is possible and desirable. This will allow comparison of results of different workers. Table I is a list of various mammals and the number of skeletal elements included in the estimate. Individual teeth of small rodents are not included as is also the case with foot elements of most rodents because of their small size or difficulty of assignment. Vertebrae and ribs are excepted for all mammals. It should be noted that when dental elements are counted in the determination of the estimate they should be included when making the actual count even when they occur in a jaw. Thus, a complete left lower jaw of a felid would be counted as nine specimens if all the teeth are in place. This is important because of the later use of this figure in determining the relative completeness of representation.

The estimates in Table I are intended for later Tertiary mammals and will have to be somewhat altered for earlier Tertiary forms especially those experiencing a loss or fusion of elements in their later history.

The estimates presented here are in some cases

TABLE I. Estimated number of elements of some late Tertiary mammals

	Scapanus	*Hydroscapheus*	sloth	chiropterids	rabbits	mylagaulids	sciurimorph rodents	large myomorphs	small myomorphs	canids	mustelids	felids	equidae	rhinos	proboscideans	peccaries	oreodonts	camels	antilocapridae
upper molars	....	....	6	....	6	4	6	6	....	4	2	2	6	6	2-4	6	6	6	6
lower molars	....	....	6	....	6	4	6	6	....	6	4	2	6	6	2-4	6	6	6	6
upper premolars	....	....	....	....	4	2	2	....	....	8	6	6	6	6	....	6	8	8	6
lower premolars	....	....	....	....	2	2	2	....	....	8	6	6	6	6	....	6	8	8	6
upper canines	....	....	2	....	....	....	....	....	....	2	2	2	....	2	....	2	2	2	....
lower canines	....	....	2	....	....	....	....	....	....	2	2	2	....	2	....	2	2	2	....
upper incisors	....	....	....	....	2	2	2	2	2	6	6	6	6	4	2	4	6	....	....
lower incisors	....	....	....	....	2	2	2	2	2	6	6	6	6	....	0-2	4	6	6	6
mandible	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
skull	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
scapulae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
humeri	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
radii	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
ulna	2	2	2	....	2	2	2	2	2	2	2	2	2	2	2	2	2	....	....
carpals	....	....	14	....	....	....	....	....	....	14	14	14	14	14	14	14	14	14	14
metacarpals	....	....	10	....	....	....	....	....	....	10	10	10	6	10	10	4	8	2	2
phalanges	....	....	18	....	....	....	....	....	....	10	10	10	4	10	12	8	16	4	4
hoofs	....	....	....	....	....	....	....	....	....	....	....	....	2	8	....	4	6	4	4
pelvis	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
femura	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
tibia	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
fibulae	....	....	....	....	....	....	....	....	....	2	2	2	....	....	2	2	2	2	2
astraguli	....	....	2	....	2	2	2	2	....	2	2	2	2	2	2	2	2	2	2
calcania	....	....	2	....	2	2	2	2	....	2	2	2	2	2	2	2	2	2	2
other tarsals	....	....	14	....	....	....	....	....	....	10	10	10	8	10	10	4	10	6	6
metatarsals	....	....	6	....	....	....	....	....	....	10	10	10	6	10	10	4	8	2	2
phalanges	....	....	10	....	....	....	....	....	....	10	10	10	4	10	12	8	16	4	4
hoofs	....	....	....	....	....	....	....	....	....	....	....	....	2	8	....	4	6	4	4
Totals (Est. no. elements)	17	17	109	15	43	37	41	37	21	129	121	119	103	133	103	109	151	99	91

quite different from those indicated earlier (Shotwell 1955). Because of this, the faunal analysis diagrams for McKay Reservoir and the Hemphill have been recalculated and appear here in Table II and as Figures 1 and 2. The results are little different from those presented earlier. A standard number of elements of 100 was used instead of 57 as previously. This makes the calculations simpler. The corrected number of specimens is then found from:

$$\frac{\text{Number of specimens} \times 100}{\text{estimated no. elements}}$$

SMALL SAMPLE EFFECTS

In the original demonstration of the method, samples were studied from two quarries, McKay Reservoir, Oregon, and Hemphill, Texas. These were large samples, one over 750 specimens, the other over 3200 specimens. Although concentrations of fossil mammals of comparable density are not uncommon, they are rare enough to encourage the worker to determine of what value smaller samples may be. Two types of small samples are most commonly encountered in the field. One may

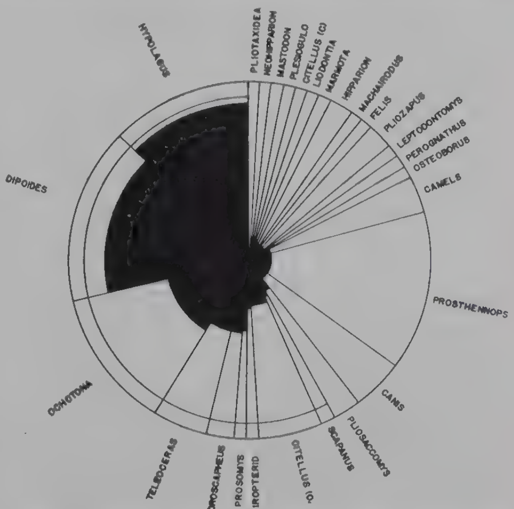

FIG. 1. Faunal Analysis Diagram of the McKay Reservoir Oregon fauna. The concentric line includes the mammals of the proximal community. The relative abundance of forms is indicated by the width of the section of the pie portion of the diagram. The radial depth of each bar indicates the completeness of representation of that species.

TABLE II. Basic data of Hemphill and McKay Reservoir

Locality.....	HEMPHILL			McKAY RESERVOIR			McKAY (small quarry sample)			McKAY (small float sample)		
Genus	No. sp.	No. ind.	Cor. sp. ind.	No. sp.	No. ind.	Cor. sp. ind.	No. sp.	No. ind.	Cor. sp. ind.	No. sp.	No. ind.	Cor. sp. ind.
Scapanus	.....	...	....	2	1	11.7	..	..	...	..	.	...
Hydroscapheus	.....	...	....	7	2	20.6	1	1	5.9	..	.	.
Sloth	5	2	2.3	...	..	....	..	..	....	..	..	..
Chiropterid	.....	...	....	2	1	13.3	..	..	....	..	..	..
Hypolagus	24	3	18.9	203	11	42.9	20	2	23.3	23	2	26.7
Ochotona	.....	...	....	17	11	22.1	5	2	35.7	4	2	28.5
Liodontia	.....	...	....	1	1	2.4	..	..	....	..	..	..
Mylagaulus	16	3	13.6	...	..	....	1	1	2.7	1	1	2.7
Marmota	.....	...	....	3	2	3.7	..	..	....	1	1	2.4
Citellus (O)	.....	...	....	25	5	12.2	11	2	13.4	5	2	6.1
Citellus (C)	.....	...	....	1	1	2.4	..	..	....	..	..	....
Pliosaccomys	.....	...	....	4	2	9.5	2	1	9.5	1	1	4.8
Perognathus	.....	...	....	1	1	4.8	..	..	....	..	..	....
Leptodontomys	.....	...	....	1	1	4.8	..	..	....	..	..	....
Dipoides	.....	...	....	219	14	38.2	22	2	26.9	35	2	42.7
Castor	.....	...	....	...	..	....	..	..	....	1	1	2.4
Prosomys	.....	...	....	4	1	19.1	..	..	....	..	..	...
Pliozapus	.....	...	....	2	2	4.7	1	1	4.8	.	..	...
Plesiogulo	2	1	1.7	2	1	1.7	..	..	....	.	..	..
Mustela	.....	...	....	...	..	....	1	1	4.8	.	..	.
Pliotaxidea	.....	...	....	1	1	0.8	..	..	....	.	.	
Osteoborus	362	15	18.7	7	1	5.4	2	1	1.6	..	..	....
Canis	10	1	7.8	34	4	6.6	9	1	7.0	4	1	3.1
Vulpes	18	2	6.9	...	..	....	..	..	..		.	
Agriotherium	11	1	8.5	...	..	....		..	..	.	.	.
Felis	.....	...	....	5	1	4.2	.			.		..
Machairodus	108	3	30.2	5	1	4.2	..	..	....	..	.	..
Hipparion	.....	...	....	10	3	3.2	3	1	2.9	1	1	0.9
Neohipparion	126	3	40.7	1	1	0.9	..	..	....	..	.	.
Nannippus	191	5	37.1	...	..	....		..	..	.	.	
P. Astrophippus	224	7	31.1	...	..	...		.	..	.	.	.
Pliohippus	1,157	63	17.8	...	..	..	..	..	....	..	..	.
Aphelops	374	9	31.3	...	..	....	..	..	....	..	..	
Teleoceras	1	1	0.8	108	4	20.6	6	1	4.5	6	1	4.5
Prosthennops	65	5	11.9	69	11	5.8	11	1	10.1	12	2	5.5
Pediomeryx	40	3	14.3	...	..	....	..	..	....	..	..	...
Pliauchenia	416	21	19.6}	16	3	5.3	..	..	....	1	1	1.0
Paracamelus	37	3	12.2}									
Alticamelus	22	3	7.3	...	..	....	..		...		.	
Mammut	8	2	4.1	1	1	1.0		..	..	.	.	. .
Capromeryx	42	2	22.6	...	..	....		.	. .	..	..	.
	3,259	158		751	88		95	18		95	18	

be termed the small quarry sample, that is a situation in which the material is collected in place but in a limited concentration. Another is the occurrence of specimens loose on the surface in a limited area with no concentration of material in place evident. Samples of this type are usually called "float."

The relation of small sample results to those of large ones may be indicated by taking small samples of both types described above from a locality which has produced a large sample previously analyzed. This is the method used here by recollecting at the McKay Reservoir, Oregon, site. A fresh quarry sample was taken using the same methods employed in the original excavation. The float sample was collected a year after first clearing the surface of the locality of all float so that the sample collected was a result of weathering over the year's time and was not influenced by earlier work. Each of these samples numbered about one hundred specimens. Caution is required in collecting float samples to insure that the materials are derived from a single lentil in a limited area and that all specimens are collected, otherwise contamination from other environments will result.

The small samples were analyzed in the same way as the large one earlier. The results are presented in Table II and Figures 3 and 4. The faunal analysis diagram of the larger sample appears in Figure 1. The members of the proximal community present in the samples are listed below:

Large Quarry	Small Quarry	Float Sample
Hypolagus	*Hypolagus*	*Hypolagus*
Dipoides	*Dipoides*	*Dipoides*
Ochotona	*Ochotona*	*Ochotona*
Teleoceras	*Citellus*	
Hydroscapheus	*Prosthennops*	
Prosomys		
Chiropterid		
Citellus		
Scapanus		

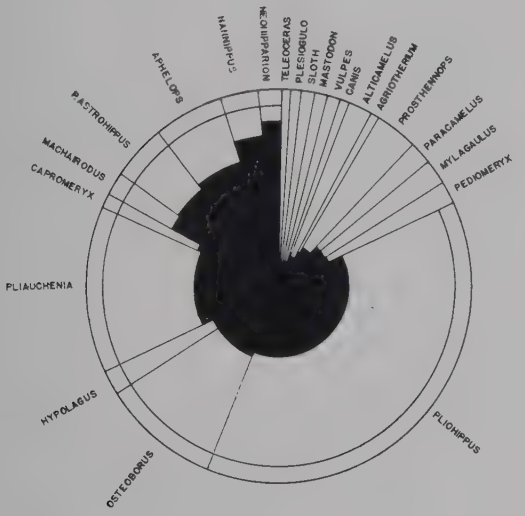

FIG. 2. Faunal Analysis Diagram Hemphill Texas Fauna.

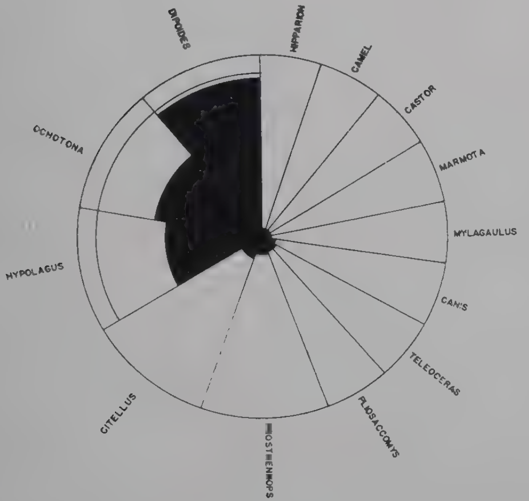

FIG. 3. Faunal Analysis Diagram of small float sample from McKay Reservoir.

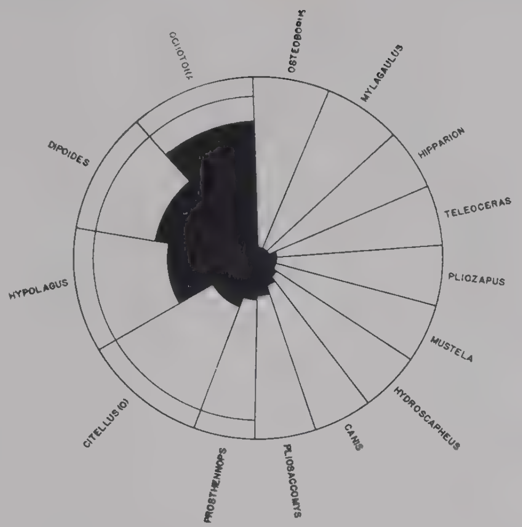

FIG. 4. Faunal Analysis Diagram of small quarry sample from McKay Reservoir.

It is clear from the three diagrams that the same proximal community is indicated. The small samples, as might be expected, did not produce as complete a list of the members of the proximal community as the large sample. They also (Small Quarry Sample) include members not assigned to the proximal community as a result of analysis of the large sample. In the present approach the position of a mammal on the faunal analysis diagram is determined by the corrected number of specimens per individual representing it in the sample. Mammals with higher than average ratios are considered to be members of the proximal community. In small samples, however, the number of individuals (indicated by the minimum number) may not be over two for any mammal present in the sample. (See Table II.) As mentioned earlier the minimum number is the smallest number of individuals necessary to account for the material of any species in the sample. However, the presence or absence of a single specimen may determine whether the resultant minimum number is one more or one less in size. The effect this has on the number of specimens per individual is shown in Figure 5. The percent of difference in the number of specimens per individual due to a difference of one in the determination of the minimum number is high when the minimum number is less than three; above three the difference is greatly reduced. Thus, samples in which the majority of the forms represented have a minimum number of less than three are more likely to produce anomalous community membership lists than those with predominantly higher minimum numbers. It is apparent, however, that although some small sample effects are to be expected in these

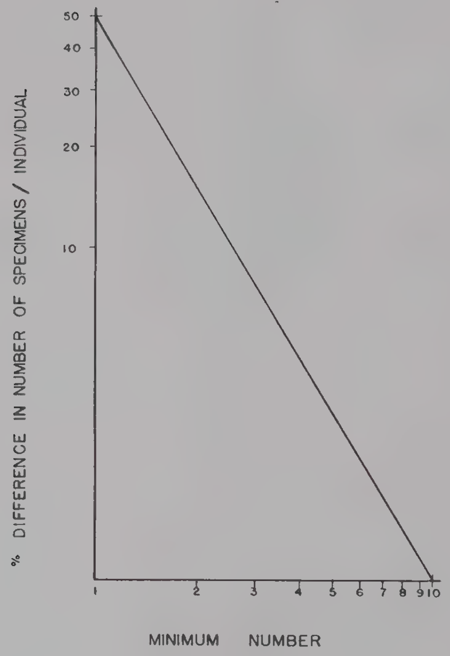

Fig. 5. Change in the percent of difference in number of specimens per individual at various minimum numbers when an error of one in the minimum number is introduced.

collections they are of value as indicators of a community previously analyzed. More detailed study of the community must be reserved for larger samples. It should also be noted that carefully collected float samples may be as useful as those from a quarry.

Inter-Community Relationships

It is a common occurrence to see quite different faunal lists from localities of about the same age. The differences may be due to one or more of several major causes, including geographic separation, inequality of age, and variation in environment. If the first two of these sources of faunal difference can be eliminated then those differences due to environmental conditions may be studied with more assurance. The present study is concerned with the diversity of communities presented when a number of faunules of the same age and biologic province are examined. The occurrence of a relatively thin flat lying sedimentary unit of limited geographic extent in northeastern Oregon presents an ideal situation for this study. A number of localities have been established in this unit. These localities occur south and east of the town of Arlington, Oregon. The map (Figure 6) indicates their positions. The two faunules just southeast of Arlington are referred to as the Krebs Ranch faunules 1 (UO2322) and 2 (UO2323). The Boardman faunule (UO2255) occurs four miles southwest of Boardman, Oregon, and the Westend Blowout faunule (UO2349) twelve miles southwest of Hermiston, Oregon.

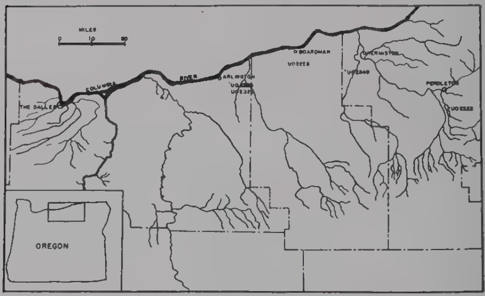

Fig. 6. Map of Northeast Oregon showing the positions of the sites discussed.

Also shown on the map is the McKay Reservoir local fauna (UO2222) south of Pendleton, Oregon. All these except the McKay Reservoir occur in the same relatively thin stratigraphic unit indicating their contemporaneous or near-contemporaneous age. Many of the genera which occur at McKay Reservoir are also found at the Krebs Ranch, Boardman, and Westend Blowout sites. The McKay Reservoir fauna may be slightly older than the others. The local geologic relationships do not allow a confirmation of this because of the lack of superposition of the two units containing the faunas. In any event the ages are not greatly different. The McKay Reservoir fauna is discussed here because of its later aid in interpreting the results of this study.

A morphologic description of the mammals in the new fauna and their stratigraphic relations to other local faunas is being prepared and will appear later. An extended discussion of this aspect of the fauna has no place in the present study.

The stratigraphic unit containing these faunules consists of unconsolidated sands, tuffaceous sandstone and tuffs. The strong prevailing westerly winds attack these sediments. The resultant deflation produces long east-west depressions with dunes of the excavated sediment at the east end. These depressions are locally called "blowouts." They vary from a few feet to a mile or more in length. The deflation of the fine sediment acts as a giant screening operation and produces a concentration of fossils at the bottom of the blowout. The faunules studied here were collected from these blowouts. Krebs Ranch No. 1 was collected

TABLE III. Basic data of Krebs Ranch 1 and 2, Westend Blowout and Boardman localities

Locality....	KREBS RANCH 1			KREBS RANCH 2			WE TEND BLOWOUT			BOARDMAN		
Genus	No. sp.	No. ind.	Cor. sp. ind.	No. sp.	No. ind.	Cor. sp. ind.	No. sp.	No. ind.	Cor. sp. ind.	No. sp.	No. ind.	Cor. sp. ind.
Scapanus	..	..	....	3	2	8.8	2	2	5.9	...	..	...
Sloth	..	..	....	...	..	.....	5	1	4.5	10	1	8.85
Hypolagus	45	2	52.4	30	2	34.8	49	10	11.4			....
Citellus	6	2	7.3	76	5	35.2	116	12	23.6			..
Peromyscus	2	2	4.8	2	2	4.75	...			.		
Perognathus	..	..	....	2	1	9.5	...	..	...	.	.	..
Castor	..	..	....	...	..	.....	1	1	2.4	.		.
Dipoides	35	2	42.7	1	1	2.5	...	..	....	...	..	....
Canis	2	1	1.5	6	1	4.65	17	2	6.6	13	1	10.6
Osteoborus	..	..	....	...	..	.....	...	..	....	49	4	9.5
Machairodus	..	..	....	...	..	.....	...	..	....	2	1	1.7
Bassariscus	..	..	....	...	..	.....	2	2	0.8	4	1	3.1
Pliotaxidea	..	..	....	...	..	.....	8	2	3.3	...	..	.....
Plesiogulo	..	.	....	...	.	....	...	.	..			.....
Bear	..	..	....	...	..	.....	2	1	1.6	3	1	2.33
large carnivore	..	..	....	...	..	.....	24	1	18.6	...	..	....
Teleoceras	..	..	....	3	1	2.3	26	2	9.8	4	1	3.0
Aphelops	..	..	....	...	..	.....	...	..	....	39	2	14.6
Neohipparion	..	..	....	...	..	.....	...	..	....	104	3	33.7
Pliohippus	..	..	....	1	1	0.9	5	1	4.9	...	..	.....
Mammut	..	..	....	1	1	1.0	97	1	97.0	6	1	5.72
Prosthennops	1	1	0.9	13	2	5.5	107	5	19.6	76	3	23.3
Sphenophalos	..	..	....	...	..	.....	...	..	....	144	5	31.6
Camel L	..	..	....	...	..	.....	47	2	23.3	7	1	6.93
Camel S	..	..	....	7	1	6.9	41	3	13.5	215	20	10.6
Totals	91	10		145	20		549	48		676	45	

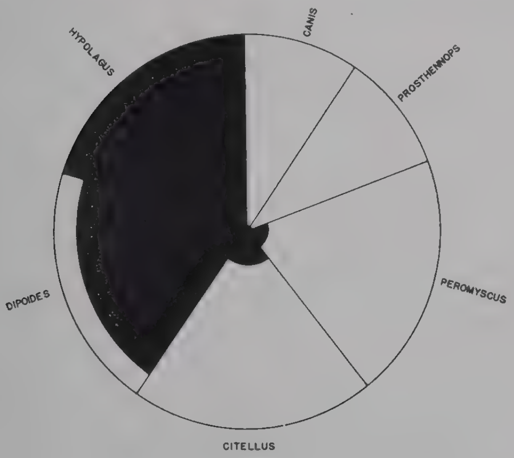

FIG. 7. Faunal Analysis Diagram Krebs Ranch No. 1 faunule.

from a very small blowout, whereas the Boardman and Westend Blowout localities were found in larger ones. Careful collection on hands and knees produces what is believed to be a reliable sample. All of the materials save those from the Boardman site were collected by field parties of the Museum of Natural History of the University of Oregon under the author's direction. At Boardman the collection was made by Mr. Grattan L. Hoffmann of Boardman and is part of his private collection. Discussion with Mr. Hoffmann over the past six years has convinced the author that the collection was made with care enough to be used in the present study. However, some small mammals may have been missed. Allowance for this will be made later. The faunule collected by Hoffmann is important because it provides a sample of a community from a habitat not represented at the other localities. Re-collecting would be difficult because the area is now a bombing range.

A synopsis of the data from these four faunules is included in Table III. It will be noted that although these are all part of the fauna of this particular area and the period of time represented the occurrence and relative abundance of the species represented varies greatly from site to site. It will be shown later how each of these sites represents a different aspect of the whole fauna as reflected in a variety of communities representing as many habitats.

Analysis of the Krebs Ranch No. 1 faunule is presented in Figure 7. This is a small sample, too small to determine a community organization. However, it will be noted that it is much like the small samples from McKay Reservoir discussed above. (Figures 3-4.) The two representatives of the proximal community (the major community adjacent to the site of deposition represented by the sample) *Hypolagus* and *Dipoides* are also the important members of the proximal community at McKay Reservoir. Since *Dipoides* (Beaver) is an amphibious form there is little doubt that the Krebs Ranch No. 1 sample indicates a community very similar to that at McKay Reservoir and representing the same sort of habitat, a pond-bank association.

The sample from Westend Blowout is much larger than Krebs Ranch No. 1, and numbers about 550 specimens. Figure 8 is an interpretation of this material. The proximal community is as follows:

Pliomastodon
Camel (*Paracamelus?*)
Citellus
Camel (*Alticamelus* or *Pliauchenia*)
Large carnivore (Felid?)
Prosthennops sp. (Peccary)
Hypolagus (Rabbit)

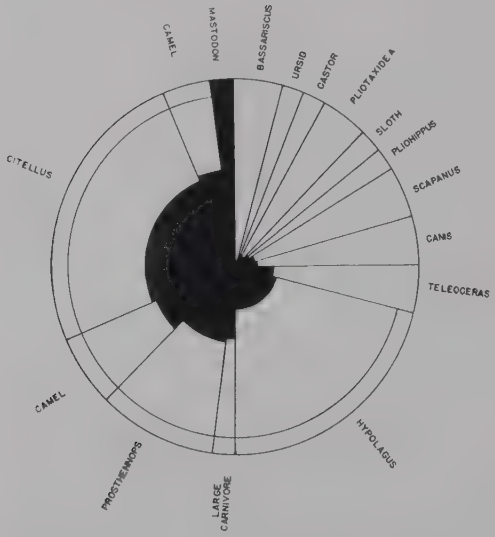

FIG. 8. Faunal Analysis Diagram Westend Blowout faunule.

It is interesting to note that in the McKay Reservoir and Hemphill faunas it was apparent that a number of mammals occurred in one or the other or both, but were not represented in either proximal community; in other words, these mammals represented one or more communities other than those considered to be proximal at McKay Reservoir or Hemphill. Several of the mammals in question are present in the proximal community at Westend Blowout. They are *Pliomastodon, Paracamelus,* and *Prosthennops*. These are browsing or omnivorous animals with low crowned teeth. They are likely to represent a woodland situation on the basis of their morphologic adaptations. This is a habitat which may be expected adjacent to either a pond or grassland, the two habitat types suggested for the proximal communities of McKay and Hemphill. This would explain the appearance of these mammals as representatives of distant communities at both places.

The sample from Krebs Ranch No. 2 (Figure 9, Table III) includes 145 specimens. This is again a small sample but is interesting in several ways. The proximal community is represented by *Citellus, Hypolagus* and possibly *Perognathus*. *Citellus* also appears as a member of the proximal community at Westend Blowout and *Hypolagus* as a member of the proximal community at both Krebs Ranch No. 1 and Westend Blowout. The mammals which appear in the faunal analysis diagram for Krebs Ranch No. 2 representing distant communities are those which are found in the proximal communities at Krebs Ranch No. 1 and at Westend Blowout. This community then is transitional between the other two.

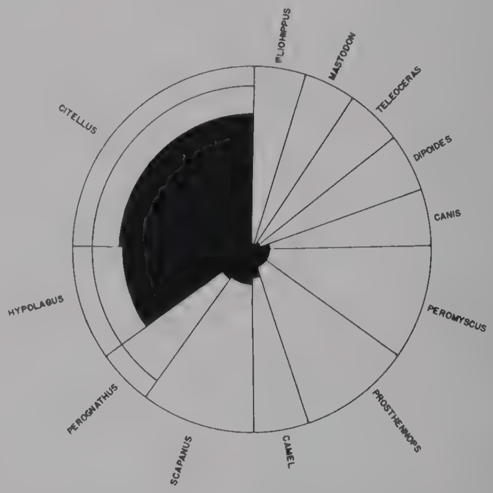

FIG. 9. Faunal Analysis Diagram Krebs Ranch No. 2 faunule.

The Boardman faunule is represented by a large sample, 676 specimens. Figure 10 is an interpretation of the sample. The proximal community includes the following:

Neohipparion (3 toed horse)
Sphenophalos (antelope)
Prosthennops (Peccary)
Aphelops (rhinoceros)
?Pliauchenia (camel)

Canis (coyote size dog)
Osteoborus (Hyaenoid dog)

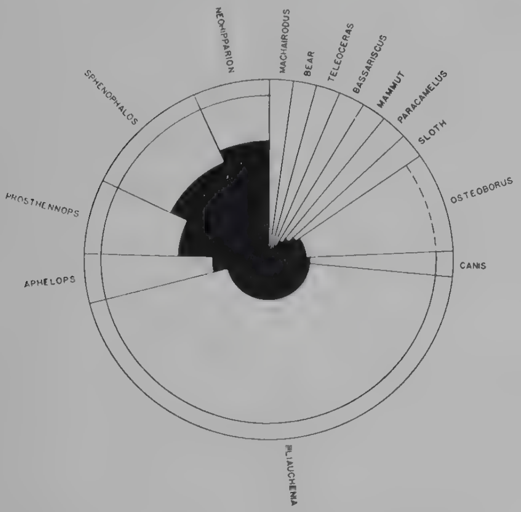

FIG. 10. Faunal Analysis Diagram Boardman faunule.

These mammals are grazing forms and their predators adapted to high speed running. This community is similar to that of the Hemphill (Figure 2). There are several notable differences. The antelope at Boardman is not of the same genus as that of the Hemphill. *Pliohippus,* a horse of major importance in the Hemphill fauna, is not in evidence at Boardman. *Machairodus* (saber-toothed cat) is not a member of the proximal community at Boardman. However, it is a rare form even in the Hemphill which is represented by a sample of nearly five times the size of the one from Boardman. The differences between the two grazing communities so far encountered are of several kinds. Their great geographical separation possibly accounts for the difference in antelopes. Sample size may explain the lack of such a rare form as *Machairodus* in the proximal community at Boardman. The lack of *Pliohippus* may be a result of several factors; the grassland of the Boardman area may have been too small in area to support *Pliohippus* or may have differed in some other way which prevented its appearance in the proximal community. This may, as suggested for the antelopes, also be a geographic difference; *Pliohippus* is unknown from early Pliocene faunas in Oregon and is not of major importance in any of the middle Pliocene faunas known north of the Northern Great Basin. The absence of *Hypolagus* is probably an artifact of collecting. These two faunas representing communities of the grassland vary in some character-

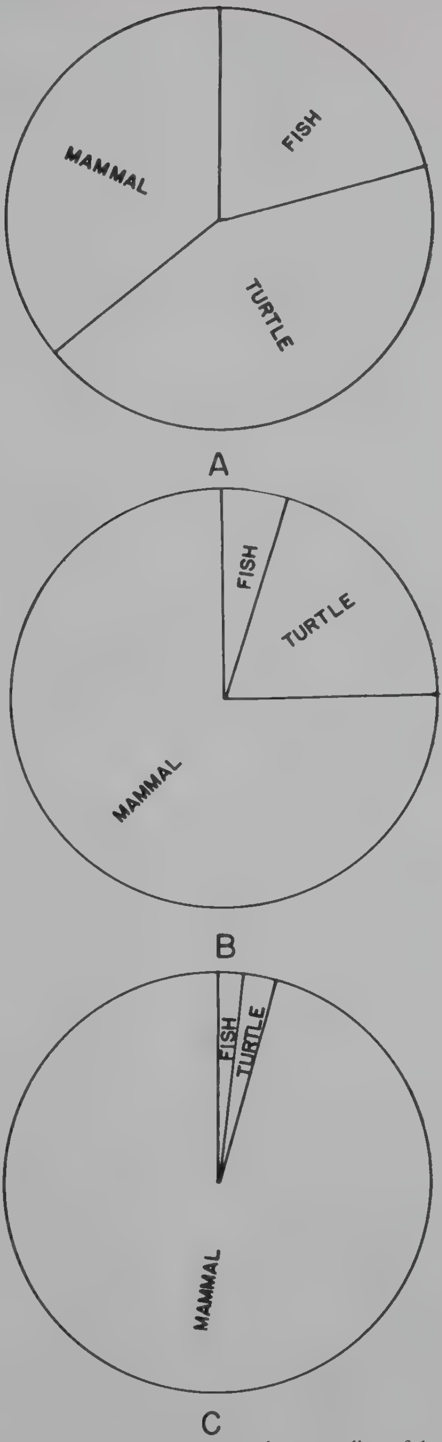

FIG. 11. Relative amounts of mammalian, fish and turtle materials at A, Krebs Ranch No. 1, B, Krebs Ranch No. 2, and C, Westend Blowout.

istics but more importantly are similar in structure.

Three of the new localities discussed here present a gradation from a largely aquatic situation (Krebs Ranch No. 1) to a terrestrial one (Westend Blowout) according to this approach. Included in these collections, apart from the mammalian material, are remains of fish and turtle. An indication of the relative aquatic or terrestrial nature of the habitat of these materials may be obtained by considering the bulk faunas. Figures 11, A, B, C, demonstrate the relative number of specimens of mammals, fish and turtle for each of the three localities discussed. The more aquatic community (Krebs Ranch No. 1, Fig. 11A), as interpreted from the mammalian material, has the largest proportion of fish and turtle, whereas the terrestrial one (Westend Blowout, Fig. 11C) has the smallest proportion. The transitional community, Krebs Ranch No. 2 (Fig. 11B), is also transitional in the proportion of fish and turtle to mammals present. These results agree with those derived from a consideration of the mammalian material alone.

Discussion

The data seen here show at least three major communities from different habitats and a fourth which is apparently a transition between two. There is no way of determining a finite number of kinds of communities one might expect in a situation such as this. Any number of variations between the several extremes could occur. The four communities discussed here are merely four possibilities encountered. If these four communities are examined in light of the fact that they are aspects of one fauna of the included geographic area at that time we can see something of the general inter-community relationships, or as might be stated, the regional community organization.

In the approach used the sample is analyzed to determine which mammals belong to the proximal community (the major community adjacent to the site of deposition) and which are chance occurrences or infrequent visitors from more distant communities. When a number of samples from such a situation as here used are from obviously quite different habitats we would expect an interdigitation of proximal and distant community members among the samples. That is, some of the mammals which appear as members of the proximal community in one of the samples should appear as members of more distant communities in the other sample. This type of inquiry was used as a test in the original discussion of the approach. However, in the original study the samples were widely separated geographically. This separation prevented any extension of the inquiry. In the series of sites discussed above geographic and stratigraphic variations have been removed. Comparison of proximal and distant communities of the examples should present a general picture of regional community organization in this particular place and time.

Since these samples all came from the same stratigraphic unit conditions of preservation should be somewhat similar. Comparison of the average of ratios of the number of specimens to the number of individuals shows this to be the case. Figure 12 is drawn using the corrected number of specimens per individual as the basis for the thickness of the bars. This number is used originally in separating the communities, proximal and distant, and so is the best basis for such an illustration. The thickness of the bars does not indicate relative abundance or population density and is not intended to. The figure is an attempt to show the relationships between the communities studied noting the occurrence of members from outside communities as occasional visitors or as appearing by chance in the deposit. The portion of the bar indicating a mammal as a member of a proximal community is solid. Where the mammal is known only as a member of a distant community, it is dotted. In the column under Krebs Ranch No. 1 several forms are shown which were not present in the sample. The collection from Krebs Ranch No. 1 was small but very much like the small samples from McKay Reservoir. This indicated a probable similarity of the proximal community of Krebs Ranch No. 1 to that of McKay Reservoir. In order to demonstrate more adequately the interdigitation of communities several mammals which probably would have appeared in a larger sample were added to the list. *Hypolagus* is listed in the Boardman faunule although it does not actually occur in the sample. Collecting methods at this locality, as mentioned above, probably missed some small mammals. The Hemphill fauna sample showed *Hypolagus* as a member of the proximal community in a similar environment. For this reason *Hypolagus* is included here.

The relative abundance of various mammals in their communities can be seen on the faunal analysis diagrams for each sample (Figures 7, 8, 9, 10). Mammals which do not appear on any of the faunal analysis diagrams as members of a proximal community are not shown in Figure 12.

The faunules illustrated are quite different from each other in their faunal list and community

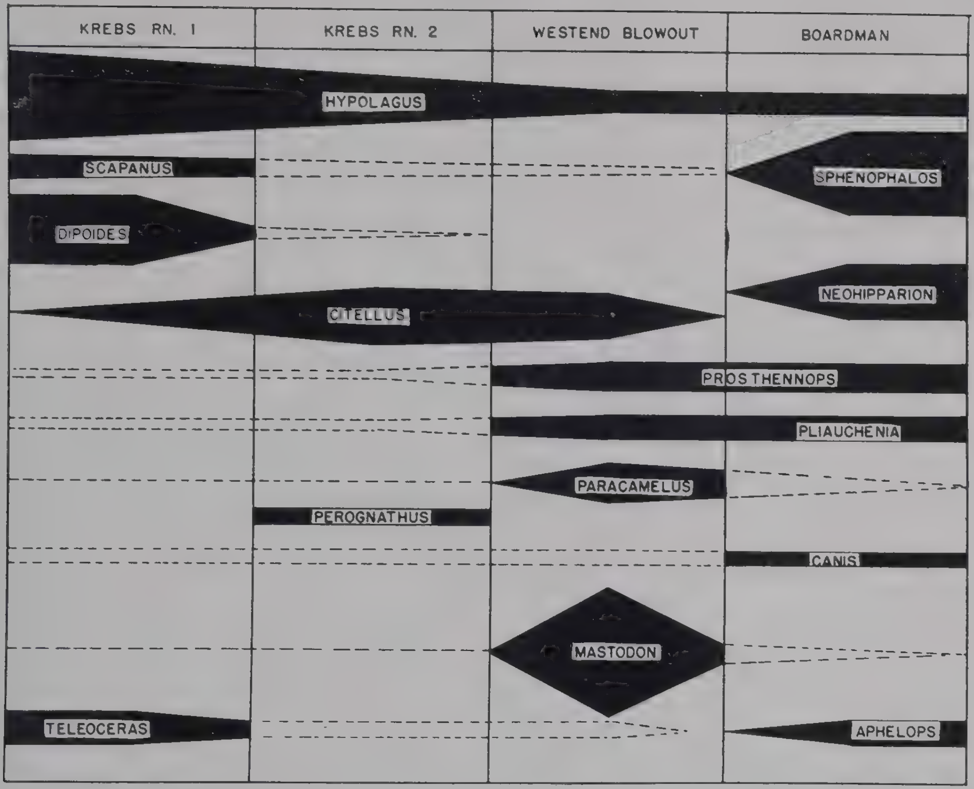

Fig. 12. Intercommunity relationships of faunules studied. Solid bars indicate presence in the proximal community, dotted portions indicate occurrence by chance or as an infrequent visitor from a distant community. Graph is constructed using completeness of representation as basis.

structure. Those at the extremes of the diagram for instance, have very few species in common. Examination of the structure of intermediate communities demonstrates an overall continuity of which these variations are a part. The illustration (Figure 12) is the regional community organization of a particular area at a particular time. It demonstrates the distribution of mammals from community to community. Some are restricted to a particular community type, others are found in several and a few are found in all the communities studied. These paleoecologic results are comparable with those from studies of living biota.

Our picture of regional community organization of mammals of the Hemphillian may be broadened to a greater portion of North America by including the data from the Hemphill fauna of Texas and McKay Reservoir. Figure 13 illustrates a generalized community organization of North American Hemphillian mammals as shown in three extremes of habitat. Examination of more samples will undoubtedly extend this information.

Community dynamics may be studied by examination of changes in community organization through time. These can be seen to advantage during times of climatic change, of intensive intercontinental faunal interchange, and of extinction of particular morphologic types. In western North America changes of all of these sorts occurred within the time-span from late Miocene to late Pliocene. If such a sequence is studied with adequate stratigraphic and geographic control, a picture of faunal change emerges that may be termed community evolution.

The author has for the last several years been engaged in a long range project such as that described above. The method described earlier and applied in the present paper is used. It is hoped that a better understanding of extinction, faunal interchange and evolution of community organization in mammals will result from the data produced by this approach.

Reference

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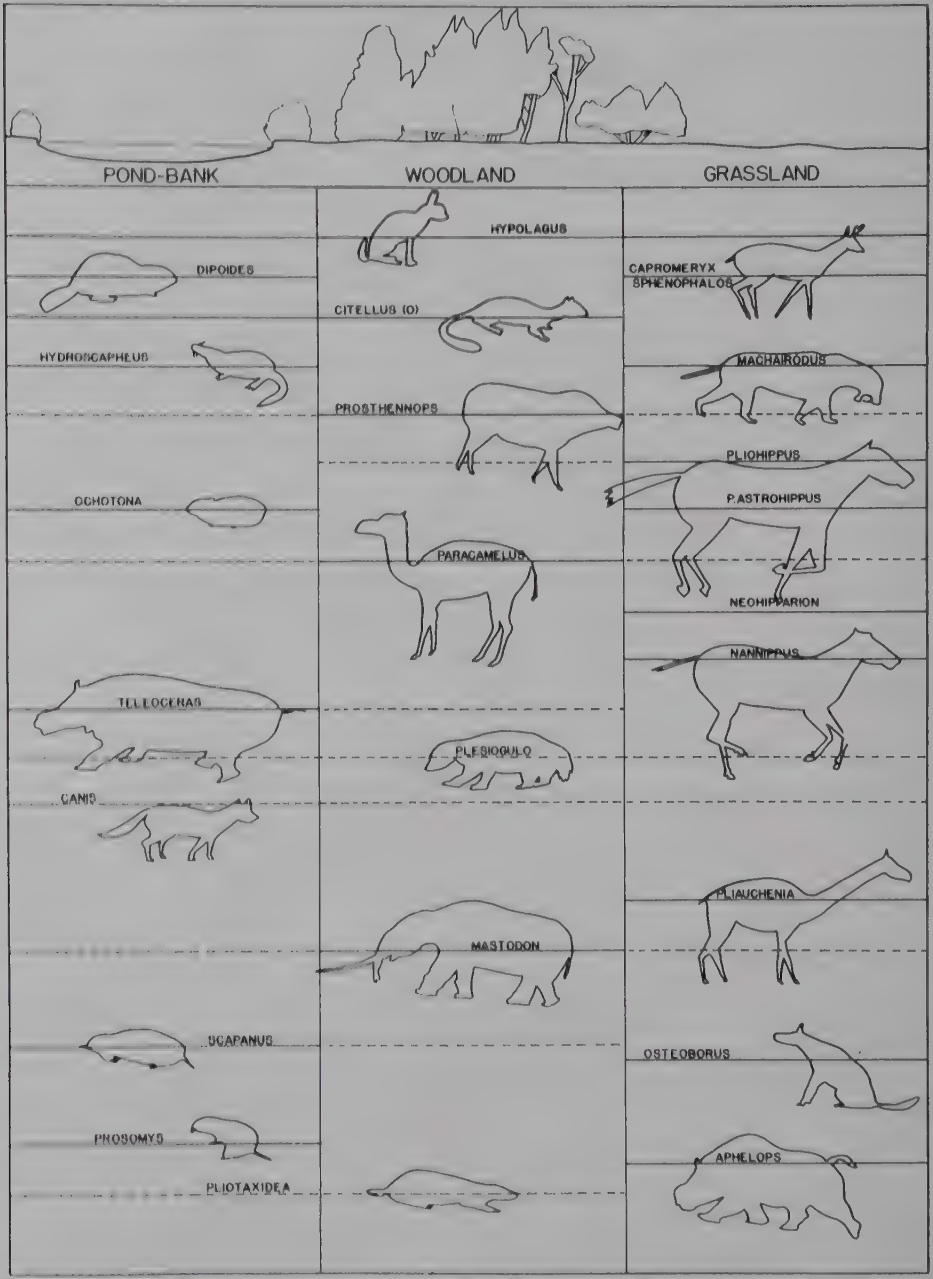
POND-BANK
WOODLAND
GRASSLAND
DIPOIDES
HYDROSCAPHEUS
OCHOTONA
TELEOCERAS
CANIS
SCAPANUS
PROSOMYS
PLIOTAXIDEA
HYPOLAGUS
CITELLUS (O)
PROSTHENNOPS
PARACAMELUS
PLESIOGULO
MASTODON
CAPROMERYX
SPHENOPHALOS
MACHAIRODUS
PLIOHIPPUS
P. ASTROHIPPUS
NEOHIPPARION
NANNIPPUS
PLIAUCHENIA
OSTEOBORUS
APHELOPS

Fig. 13. General community organization of Hemphillian mammals of three major habitats.

REACTION OF FISH (*EUCINOSTOMUS GULA*) TO ENVIRONMENTAL CHANGES[1]

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Introduction

Among icthyologists it is common knowledge that many fish in their natural habitat, or in captivity, will retreat from large objects which are suddenly introduced into their aquatic environment. It is also known that certain fish are very curious and will approach, visually orient toward, and touch novel objects after a period of adaptation. In addition, it is known that fish in aquaria are much more sensitive to environmental changes than they are in the waters of their natural habitat. These sensitive reactions to stimulus changes are inevitable concomitants of laboratory studies of captive animals and cannot be overlooked in the analysis of their behavior. Despite the ubiquity of these phenomena, we could discover no experimental studies which have attempted to quantify them. Consequently, the present experiment was designed to investigate the spatial and temporal distribution of behavior of one species of captive fish to certain environmental changes.

Procedure

Sixty fish (*Eucinostomus gula* Cuvier & Valenciennes) were subjects of this study. Their average standard length was 51 mm (range: 44-58 mm). The subjects were obtained by seining the shallow water along the shores of Bimini Harbor. When caught, several animals were placed together in storage tanks to await testing. After testing, each subject was measured and preserved in formalin. All animals were tested between the tenth and 24th of August, 1954.

The testing tank (Figure 1) was similar in size, shape, and construction to the storage tank, and was illuminated from above by a 20 watt bulb mounted in a reflector. A stream of fresh sea water was constantly running through the tank at a rate of 600 cc/min. The water temperature ranged from 28.5° C to 31.75° C during the course of the experiment, with an average reading of 30.0° C.

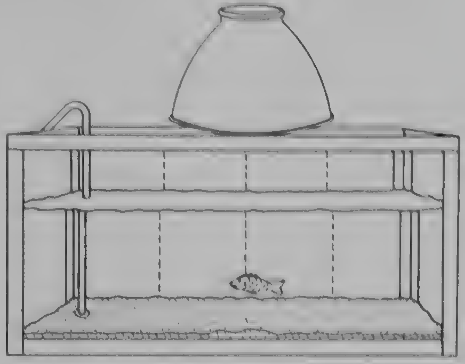

Fig. 1. Testing situation. Tank dimensions: 60 mm x 30 cm x 30 cm. The height of the water was maintained at 19 cm. The water inlet is situated near the bottom at the far left of the tank. The water outlet is situated at the surface in the center, also at the left.

Three sides of the tank were masked with brown wrapping paper. A screen with a viewing slot was placed against the fourth side of the tank, and the experimenter observed the subject through cheese cloth which covered the slot. The testing room was kept dark during the testing period, and the cheese cloth thereby functioned as a one way vision screen. The bottom of the tank was covered with approximately 12 mm of sand. A masking noise was provided by a large electric fan.

Although these fish tend to aggregate in their natural habitat, one fish was tested at a time. It was retrieved from the storage tank with a small net and jar, and was placed into the experimental tank at the far left between the water inlet and outlet. One experimenter, observing the interior of the tank through the slot, described the behavior of the fish. The other experimenter, with the aid of a stop clock, recorded the descriptions in shorthand notes on a data sheet which was marked off into successive five-second intervals.

The same procedure was followed with every animal. Each animal was observed for forty consecutive minutes. After being placed in the tank, the animal was not disturbed for the first twenty minutes. An object was then introduced into the far right corner of the tank and was left there for ten minutes. It was subsequently removed, and no further disturbances occurred during the last ten minutes of the session. The subject was then removed and the water temperature was recorded.

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[1] This study was carried out at the Lerner Marine Laboratory, Bimimi, B.W.I. This laboratory is operated by the Department of Fishes and Aquatic Biology, of the American Museum of Natural History. The authors are grateful to Dr. Charles M. Breder, Jr. for his many helpful suggestions in the preparation of this manuscript.

The environmental changes with which we were concerned during the testing session occurred (a) when the animal was initially introduced into the testing tank (b) when the object was subsequently introduced and (c) when the object was removed.

The object consisted of a band of aluminum, 9 cm wide, bent into a figure eight and painted red and black in a mottled pattern. The object stood about 18 cm tall, and was about 9 cm square in cross section. Two sides of the object were open so that the fish could enter it.

Of the sixty animals studied, thirty were tested sometime between 15 minutes and 5¾ hours after being caught. The other thirty were tested after spending 4⅔ to 7 days in captivity. These two groups are referred to as Groups 1 and 5 respectively. In each of these two groups, fifteen animals were tested during the day (D) and fifteen at night (N). The four subgroups thus formed are hereafter designated as 1D, 1N, 5D and 5N.

The data for each fish consist of sequential records of its location in the tank. In analysis of the data, an activity measure and a location measure were abstracted from the records. The spatial location of the animal was specified perceptually by viewing the animal against vertical lines drawn on the brown paper of three sides of the tank. These lines divided the tank into four sections (hereafter referred to as quadrants) = quadrant 1 on the left, quadrants 2 and 3 in the middle, and quadrant 4 on the right (Figure 1). Similarly, whether or not the animal was at the front (A) or the back (B) of the tank could be specified. Thus, a total of eight sections (hereafter called octants) could be identified. The unit of activity was the number of successively different octants entered. The fish were always introduced into octant 1B, and the object into 4B. When the record was analyzed with respect to time, the temporal-spatial distribution of activity could be specified.

The statistical significance of the results reported below were tested by the Sign Test (Dixon and Massey 1951). In the analysis of the data, the activity or location of an animal during one minute was compared with its activity or location during some other minute (listed above the columns of the tables). The paired scores of several animals were grouped and the Sign Test was then applied. The two-tailed test of significance was used throughout.

RESULTS

Activity

When the animals were first introduced into the tank, 53 out of 60 fish sank immediately to the bottom and remained there quietly for ten seconds or more. During the undisturbed periods, the amount of activity gradually increased. When the object was either introduced or removed from the tank, there was an immediate decrease in activity. Figures 2 and 3 present the average activity trends of the four groups. The points in these charts are plotted for 40 successive minutes. The object was introduced between minutes 20 and 21, and was removed between minutes 30 and 31 (indicated by the arrows in the figures). Table I indicates the statistical significance of these activity changes (a) during the first twenty minutes (min one and 20), (b) when the object

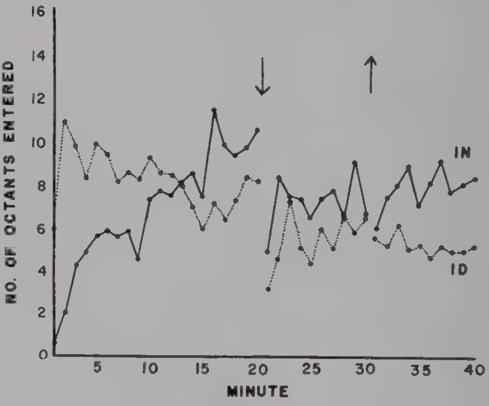

FIG. 2. Activity trend. Total no. of octants entered by groups 1D and 1N during 40 successive minutes. Each point on the curves represents a group average (N 15). Arrows indicate times when object was introduced or removed.

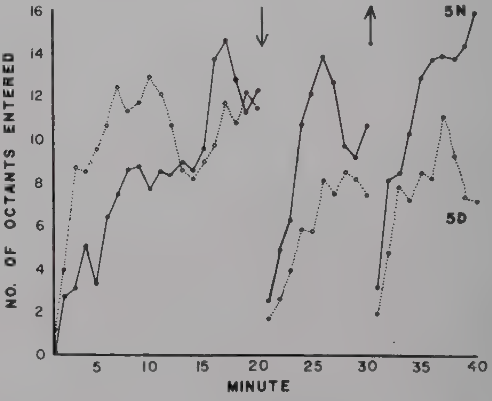

FIG. 3. Activity trend. Total number of octants entered by groups 5D and 5N during 40 successive minutes. Each point on the curves represents a group average (N 15). Arrows indicate times when object was introduced or removed.

was introduced (min 20 and 21), (c) during the time when the object remained in the tank (min 21 and 30), (d) when the object was removed (min 30 and 31), and (e) during the last ten minutes of the session (min 31 and 40). In this table, the data from the four subgroups were considered two at a time, yielding four sets of data as follows: (a) animals tested on day 1 (D and N subgroups combined), (b) animals tested on day 5 (D and N subgroups combined), (c) animals tested by day (1 and 5 subgroups combined), and (d) animals tested by night (1 and 5 subgroups combined). This table lists the probability (P) values for each comparison as well as the number (N) of observations in each test.

TABLE I. Probabilities of differences in activity changes over time

Group		MINUTES 1-20	20-21	21-30	30-31	31-40
1	P	.01	.01	.10	.10	.05
	N	25	23	24	25	27
5	P	.01	.01	.01	.01	.01
	N	24	25	23	24	26
D	P	.01	.01	.05	.10	.05
	N	23	23	23	24	26
N	P	.01	.01	.01	.01	.01
	N	26	25	24	25	27
Direction of change.........		inc.	dec.	inc.	dec.	inc.

Activity during each minute was measured in terms of the number of successively different octants entered in that period of time. There were only three comparisons which were not significant at the .05 level or better. It will be noted that the direction of change in each column is the same for each group.

How long (in terms of total number of 5-second periods) every animal remained in a single octant just before and just after each environmental change was also ascertained. Pairs of scores were obtained by comparing these successive duration measures. The pairs of duration scores of all sixty animals were assembled and the Sign Test was applied. In this way, it was found that there was: (a) a decrease of time spent in a single octant from the beginning to the end of the initial 20-min period ($P \leq .01$, $N = 57$), (b) an increase of time spent in an octant immediately after the object was introduced ($P \leq .01$, $N = 59$), (c) a decrease of time spent in an octant in the period during which the object remained in the tank ($P \leq .01$, $N = 54$), (d) an increase of time spent in an octant immediately after the object was removed ($P \leq .01$, $N = 56$), and (e) a decrease of time spent in an octant during the period after the object was removed ($P \leq .01$, $N = 57$).

Location

As mentioned above, when first introduced into the tank, the animals typically sank immediately to the bottom, were initially inactive, and remained in the octant into which they sank for at least 10 seconds. During undisturbed periods, the fish gradually moved away from quadrant 1 (on the left) toward quadrant 4 (on the right). When the object was either introduced or removed (always at octant 4B), the animals tended to return to quadrant 1 and move away from quadrant 4. Table II shows the statistical significance of the location changes during those same periods of time from which the activity records of Table I were taken. The method of analysis was similar to that discussed for those data. Each set of scores consisted of tabulations of how many five-second periods (during a given minute) were spent in quadrants 1 and 4. Over half of the comparisons yielded location changes which were statistically significant at the .05 level or better. In all but four of the twenty comparisons, at least one location change (toward, or away from quadrants 1 or 4) was significant at the 0.05 level. The direction of the location changes was the same for each of the four groups regardless of significance level.

TABLE II. Probabilities of differences in location changes over time

Minutes........		1-20		20-21		21-30		30-31		31-40	
Quadrants......		1	4	1	4	1	4	1	4	1	4
Group 1	P	.05	.01	.01	.01	.10	.25	.05	.50	.01	.25
	N	24	20	23	18	25	13	23	14	27	17
5	P	.25	.01	.25	.01	.25	.01	.50	.50	.50	.05
	N	24	17	23	17	23	12	22	13	22	20
D	P	.01	.01	.05	.01	.25	.05	.05	.50	.01	.05
	N	22	20	20	20	24	13	22	12	24	16
N	P	.50	.01	.10	.01	.10	.01	.50	.50	.50	.10
	N	26	17	26	15	24	12	23	15	25	21
Direction of change.........		dec.	inc.	inc.	dec.	dec.	inc.	inc.	dec.	dec.	inc.

In the above location analysis, a one-minute period was used as the unit of time for comparison.

A more specific picture of the location of the animals before and after environmental changes is obtained if a five-second period is used as the unit of time. The specific octant which was occupied during the five-second interval before and/or after an environmental change occurred was ascertained. Pairs of scores were obtained by comparing successive location measures. These pairs of scores were assembled for all sixty animals and the Sign Test was applied. By this means it was found that there was: (a) increased time spent in quadrant 4 from the beginning to the end of the initial 20-minute period ($P \leqq .05$, $N = 51$), (b) initial avoidance of those octants closest to that in which the object had just been placed ($P \leqq .01$, $N = 40$), (c) subsequent approach toward the octant which contained the object during minutes 21-30 ($P \leqq .01$, $N = 37$), (d) avoidance of those octants closest to that from which the object had just been removed ($P \leqq .05$, $N = 28$), and (e) approach toward the octant from which the object had been removed, during the last ten-minute period ($P \leqq .01$, $N = 45$).

Reaction to the object

During minutes 21-30 the object was in octant 4B of the tank. Figures 2 and 3, and Table I show that during this period there were increases in activity, and Table II shows that such activity became less confined to quadrant 1, and more localized in quadrant 4. Twenty-nine animals (out of 60) actually entered the octant in which the object stood, and 25 touched or entered the object. The following analyses were made only on the data from these animals. A comparison of the frequencies of these activities between the first and second five-minutes of this ten-minute period indicates a statistically significant increase: (a) of entries into the octant in which the object stood ($P \leqq .05$), and (b) of touches of, or entries into the object ($P \leqq .01$). The animals that touched or entered the object, or the octant in which it stood, were evenly distributed among the four subgroups.

The possibility exists that a similar increase in time spent in octant 4B may have characterized other undisturbed periods, in which case the increase of such approach from the 21st to the 30th minute would not be specifically associated with the object, but with a general increase in activity. However, further analysis of the record indicates that the increased time spent in octant 4B is related to the presence of the object. The ratio of time spent in octant 4B to total activity was compared between the first and second halves of three successive ten-minute intervals as follows: (a) the ten minutes before the object was introduced (min 11-20), (b) the ten minute "object-in" period (min 21-30), and (c) the ten minutes after the object was removed (min 31-40). It was found that there was a significant increase in this ratio ($P \leqq .05$, $N = 29$) from the first to the second five-minute halves of the "object-in" period, but not during the preceding ($P \leqq .50$, $N = 27$), nor subsequent ($P \leqq .50$, $N = 28$) ten minute periods. This indicates that there was a greater proportion of activity time spent in octant 4B while the object resided there than either before or after, when the object was absent.

There were 29 animals which entered octant 4B more frequently during the last than during the first half of the "object-in" period (min 21-30). Eleven of these were among the twelve most responsive animals (in terms of total number of octants entered during 40 minutes), thirteen were intermediate in total activity, and five were among the eleven least active animals. Thus, the amount of approach to the object is not clearly associated with the degree of activity of the fish.

Effects of "time in captivity" and of "testing time"

Comparison of Figures 2 and 3 indicates the following results:

(a) during the initial three minutes following all three environmental changes the average activity of group 5 was less than that of group 1 ($P \leqq 05$, $N = 18$). In this analysis, the average activity of the animals of group 1D during each of the first three minutes following each environmental change was compared with that during the corresponding minutes following each change of group 5D. A similar comparison was made between groups 1N and 5N. The pairs of scores thus obtained from the D and N groups for the three environmental changes were combined and the Sign Test was applied. The statistical analysis of the data in the following sections was carried out in a similar manner.

(b) Although group 5 activity exhibited greater initial inhibition, during the last six minutes following the three environmental changes the activity of group 5 had become greater than that of group 1. This result is statistically significant at the .01 level for both the D and N comparisons considered separately ($N = 15$ per group).

(c) The rate of increase in activity during the first five minutes following all three environmental changes is greater for group 5 than for group 1 ($P \leqq .05$, $N = 6$).

(d) During the initial ten minutes of the session, the D groups were more active than the

N groups ($P \leqq .01$, $N = 28$) for groups 1 and 5 tested separately.

(e) However, Figures 2 and 3 show a crossing of the D and N group activity between the 10th and 15th minute, and during the last 30 minutes of the session the N groups were significantly more active than the corresponding D groups ($P \leqq .01$, $N = 30$).

An analysis of the activity levels of individual animals indicated that there were wide individual differences in activity in each of the four groups. Thus, the fifteen most active and the fifteen least active animals were about equally distributed among the four groups. The most active animal swam through 907 octants during the 40-minute test period. The least active animal swam through only three octants. Both of these animals were in group 1D. The causes of such wide individual differences are not readily apparent. It should be mentioned, however, that such differences were not clearly associated with length of time in captivity, time of testing, water temperature, or animal size, when each of these factors was considered individually.

Although the main behavioral effects reported above are clearly associated with the main environmental changes which were presented, the possible effectiveness of differential water currents, temperature gradients, or oxygen tension variations must be considered. Water currents and vibrations were maximum: when the fish was introduced into the tank, when the object was introduced, and when the object was removed. Presumably the fish would retreat from the locus of maximal disturbance. Thus, the avoidance of the object octant could be explained in this manner. However, although the octant into which the fish was introduced was also a focus of water disturbance, the fish remained in that octant initially. In addition, the evidence reported above indicates that the visual characteristics of the object were important in eliciting approach. Such cues were probably equally important in eliciting avoidance. Further study is required to determine which specific stimulus aspects are responsible for such behavior changes.

The water temperature and oxygen tension in the tank would most closely approximate that of the natural environment in quadrant 1, where the water inlet and outlet were located. Nevertheless, the animals tended to move away from this locus in exploration of the object and the remainder of the tank.

Discussion

This has been an exploratory study which aimed to elucidate the characteristics of the reactions of fish to brief and simple forms of stimulus change. In this study, the environmental changes which were used produced avoidance or "freezing" reactions initially. Breder and Halpern (1946) have noted that fright reactions are elicited in newly captive fish (*Brachydanio*). These fish formed schools after being handled and introduced into the new captive environment. However, these reactions disappeared within a day or so. These authors found that any stimulus which tended to startle these fish, such as sudden movements, tank vibrations, and changes in illumination, also tended to elicit schooling. The fish became less reactive to such stimuli upon repetition, but these startle reactions reappeared when a sufficient time interval had elapsed.

Initially the animal was placed into a novel situation, the testing tank. During undisturbed periods, behaviorial changes were observed which are commonly referred to by the term "adaptation." The animal becomes adapted to the situation when it increases its activity and range of movement with time. A non-changing environment is apparently essential for this behavioral adaptation to occur, since retreat and "freezing" once again appear upon further novel stimulation or change (*i.e.,* introduction or removal of the object).

In the present study, only about half of the fish entered the octant containing the stimulus object. These animals were evenly distributed among the four subgroups. They consisted of some of the most as well as of the least active individuals. Approach to the object in this study has been demonstrated to be an active exploration of the object and is not due simply to an increase in activity. Breder (1950; 1954) and Breder and Halpern (1946 have also observed active approach and contact (exploration) of novel objects introduced into the aquarium. The nature of these reactions varied with the species used. Thus, *Bathygobius* usually made bodily contact with new objects whereas *Pomacentrus* seldom touched such objects. These authors also demonstrated that whether or not *Brachydanio* would approach targets moving along the outside of the aquarium wall depended on the size of the stimuli. Thus, a moving target of over 32 square inches caused retreat whereas smaller targets elicited approach.

It is our interpretation that the initially greater inhibition of the N groups is related to the fact that these fish were in a quiet, dark room at least one-half hour before testing, whereas the room was illuminated for some time before the testing of the D groups. In addition, laboratory personnel were moving about in the rooms in which the fish were kept during the day, whereas such was not the case at night. These fish are relatively inactive at night and the initial inactivity of the N groups may be related to their pre-test quiescent state. That the N group fish became more active than the D group fish as the session continued suggests that the light and/or laboratory activity prevalent during the day exert a prolonged inhibition of activity throughout the testing period.

It is possible that our failure to find greater differential effects of length of captivity may be due to the short time interval that was covered by this study. Perhaps a longer period of time in captivity might have yielded greater indications of adaptation. Indeed, in the field, where the fish inhabit familiar waters, we found only transient avoidance reactions and rapid adaptation and approach to the human body or hand, or to objects thrown or placed in the water. The factor of familiarity or degree of novelty is thus again implicated in determining spatio-temporal activity sequences.

SUMMARY

A study was made of the behavior of fish (*Eucinostomus gula*) to environmental changes. Sixty fish were observed singly in a tank through a one-way-vision screen. The spatio-temporal distribution of the activity of each fish was studied over a forty-minute period. Fifteen fish were tested by day and fifteen at night on both the first day, and after several days, of captivity. Comparisons of behavior were made before and/or after the environmental changes which consisted of entrance into the observation tank, introduction of an object into the tank, and removal of the object.

It was found that: (a) the initial reaction to such environmental changes consisted of a retreat from the locus of disturbance produced by the object, and marked reduction and inhibition of activity ("freezing"), as well as restriction of activity to a circumscribed spatial locus, (b) during periods of time when no such environmental changes occurred, there was a reversal of these trends; the animals gradually approached the locus where the stimulus change induced by the object occurred and increased their level of activity. As the amount of activity increased, it became distributed over a wider territory, (c) in the ten-minute period during which the object was present in the tank, there was an increase, from first to last, of touches or entries into the object or its immediate vicinity, (d) fish that had been in captivity a few days exhibited lesser activity during the first three minutes following the environmental changes, but during minutes 6-10 following these changes they were more active than the freshly captured fish. The increase in activity (adaptation) following environmental changes occurred more slowly in the newly captured animals, (e) animals tested at night were initially less active than animals tested by day but this difference was reversed during the last 30 minutes of the session, (f) there were wide individual differences in total activity and in activity distribution over time.

These data, together with observations of these animals in the field, suggest that amount of activity is inversely correlated with the degree of novelty of the stimulus situation.

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THE RETURN OF DISPLACED LARGEMOUTH BASS AND[1,2] GREEN SUNFISH TO A "HOME" AREA

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Introduction

It was our object to study the degree of faithfulness of "homing" in captured green sunfish (*Lepomis cyanellus* Raf.) and largemouth bass (*Micropterus salmoides* Lac.) after being displaced to a central release point. Other workers have observed this behavior in centrarchid fishes (Larimore 1952, Shoemaker 1952, Cooper 1953). However, more evidence is needed to determine the precision of homing among individuals of a population and the mechanism used by fish in finding their way. "Homing," as used herein, implies the ability of a displaced fish to orient itself in the new location, with the aid of perhaps a variety of mechanisms and stimuli, in order to return to familiar territory, which then might be recognized by "landmarks," whether detected by olfaction (Hasler & Wisby 1951, Wisby & Hasler 1954), vision (Aronson 1951, Hasler 1956a) or other senses as learned from previous experience. The perceptive mechanisms employed by fishes in migration have been pointed up recently by Hasler (1956b).

Procedure and Results

Green Sunfish

Pond 2 of the University of Wisconsin Arboretum Gardner Ponds has an area of approximately one-half acre and a maximum depth of eight feet. It is roughly rectangular in shape (Fig. 1) measuring about 75 feet by 260 feet and supports a large population of small freshwater fish, largely dominated by the bluntnose minnow (*Hyborhynchus notatus* Raf.) and the green sunfish, the latter of which are much stunted, with many individuals attaining sexual maturity at a very small size.

Initially, green sunfish were captured by angling or by use of a minnow seine at either the north or south end of the pond. The fish were marked by clipping fins so as to identify the individuals according to the end of the pond at which they had been captured. The fish were carried in an open pail and released from the east or west bank (randomly selected) at a point near the center of the pond. Table I summarizes the capture and recapture data for fish treated in this manner. As can be seen from this table, these fish demonstrated a very distinct ability to return to their capture-site upon release elsewhere in the pond. Since all of the fish from one end were given the same mark, it was not possible to determine the length of time between release and recapture. Some evidence was obtained, however, from individuals with natural, recognizable, deformities that the fish could return to the capture-site within a matter of minutes.

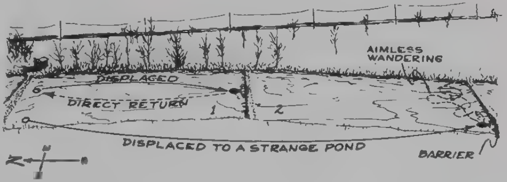

Fig. 1. A view of Ponds 1 and 2, showing their relative positions. Also illustrated is the method used in displacing the green sunfish ("buoyed," see Fig. 2) for tracking in intra- and inter-pond displacement.

Table I. Recapture data (by end) for fin-clipped green sunfish taken from Pond 2

			Recaptures at Same End as that of Capture		Recaptures at End Opposite that of Capture	
Year	Captures	Recaptures	Number[4]	%	Number[4]	%
1954	692	509	495	97	14	3
1955[1]	746	103	87	84	16	16
1955[2]	643	88[3]	79	90	9	10
All.	2,081	700	661	91	39	9

[1] Represents fish taken immediately after ice went off pond and before any new fish had been clipped.

[2] Data for all fin-clipped fish in pond recaptured in 1955 including those clipped in 1955.

[3] This figure is low because less time was devoted to recapture effort.

[4] This column in Tables I, II and III includes fishes recaptured one or more times; percentages are computed on recaptures.

Fish which were recaptured were transported again to the middle of the pond and released. It is quite likely, therefore, that some fish were recaptured more than once. The large number of individuals recaptured at any one time, however, would seem to preclude the possibility that the data represent merely a large number of re-

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turns by a small number of fish. Also, since the sampling methods (traps, seines, and angling) were not 100 percent efficient, it is certain that some fish which had returned to the capture-site were not recaptured immediately.

Of special interest is the information obtained in the spring of 1955 (Table I; 1955[1]). The fish represented in this row were originally captured and marked in 1954 before the pond froze over. Attempts to recapture these fish during the winter were, in large part, unsuccessful and the results inconclusive. No fish were present in the shallow water at the ends of the pond until almost four weeks after the ice started to leave. When they reappeared, however, they were found to be largely (84 percent) at the same end as that of their original capture; this, despite about four months of residence in the deeper portions of the pond, away from the site of capture and recapture. Since all the shallows of the pond were deserted by their summer residents, it can be assumed that fish from all parts of the pond lived in closer proximity to one another during the winter than was necessary during the summer. Ample opportunity existed for mixing, but apparently very few of these fish were permanently dislocated from the habitat which they occupied during the previous summer.

When the precision with which these fish were able to return to the site of their original capture became apparent, an attempt was made to narrow still further the area of capture and recapture. The four corners of the pond were, therefore, seined individually. The fish captured therefrom were distinctively fin-clipped, according to the corners from which they had been seined, and released at the center of the pond as with the fish reported above. Table II summarizes capture and recapture data for these fish. It is evident, from inspection of this table, that their ability to return to the capture-site continued unabated even though the area of this site had been much reduced. Also, it is striking that even these fish recaptured after a winter under the ice returned to the same habitat which they had occupied the previous summer.

TABLE II. Recapture data (by corner) for fin-clipped green sunfish taken from Pond 2

Year	Captures	Recaptures	RECAPTURES AT SAME CORNER AS THAT OF CAPTURE		RECAPTURES AT CORNER OTHER THAN THAT OF CAPTURE	
			Number	%	Number	%
1954	107	255	242	95	13	5
1955[1]	746	26	22	85	4	15
1955[2]	643	29	26	90	3	10
All	1,496	310	290	91	20	9

[1] Represents fish taken immediately after ice went off pond and before any new fish had been clipped.

[2] Data for all fin-clipped fish in pond recaptured in 1955 including those clipped in 1955.

Largemouth Bass

A study, projected to be similar in objective and scope to that on the green sunfish, was begun on the largemouth bass of two lakes in Chippewa County, Wisconsin. Riley Lake is a seepage lake, roughly oval in shape, and covers an area of about 15 acres. The other, Farm Pond No. 1, is also oval in shape but only eight acres in area. It is fed by a small brook from a neighboring lake and, in turn, delivers an intermittent stream of water to a nearby pond.

Fish were captured by angling and by fyke-netting operations from June 29 through August and, as with the green sunfish, they were fin-clipped according to the section of the lake from which they had been captured. All captured fish were then taken to the center of the lake in an open tub and released.

Attempts were made to recapture marked bass by angling and netting in the capture areas. As can be seen from Table III, these fish did not distribute themselves at random through the population, but rather, were much more likely to be recaptured at the same end of the lake as that of their original capture (68 percent) than anywhere else in the lake.

TABLE III. Recapture data for fin-clipped largemouth bass taken from two lakes in Chippewa County, Wisconsin

Site	Year	Captures	Re-captures	RECAPTURES AT SAME END AS THAT OF CAPTURE		RECAPTURES AT SITE OTHER THAN THAT OF CAPTURE	
				Number	%	Number	%
A....	1954	137	26	19	73	7	27
B....	1955	439	230	156	68	74	32
A+ B....	1954 + 1955	576	256	175	68	81	32

Site A—Riley Lake, Chippewa County, Wisconsin.

Site B—Farm Pond No. 1, University of Wisconsin Fisheries Research Area Chippewa County, Wisconsin.

As with the green sunfish, largemouth bass which had been captured and marked during the summer, were more likely to be caught the following summer in the same areas of the lake as those of their original capture (77 percent) than in any other area. It is not known to what extent these fish move about the lake during the winter, although it is known that they leave their summer areas at the lake edge. It is, of course, quite possible that they do not move very far from their "home" areas.

Speed of return of buoyed fish

Green Sunfish

In the previous procedures it can be argued that the fish reach "home" through wandering and not in a directional manner. In order to determine whether the fish were truly oriented, nesting male green sunfish were captured by hook and line in the Arboretum pond described above. A small pencil-shaped bobber was then attached to a nylon thread 3-4 feet long which, in turn, was tied to a hook. The latter was forced into the flesh at the posterior end of the dorsal fin (Fig. 2).

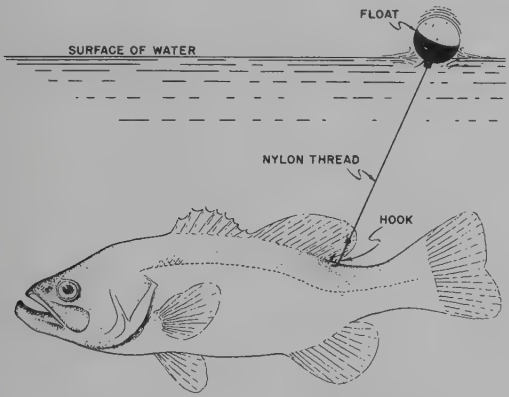

Fig. 2. Largemouth bass, showing method of attaching the float which was used as an aid to tracking the course of the fish after displacement. A nylon thread connects the bobber and hook.

The fish were then carried to the new site in an open pail and released individually at that point. The time of return to the place of capture was recorded and the course which the fish traversed was observed as the bobber was pulled along the surface. Since developing this method, we have learned that a similar technique is used by anglers to locate schools of fish after one has been caught.

The protocol (Table IVa & IVb) of the performance of these green sunfish, all of which were adult males in breeding condition, shows that they were well oriented when displaced in their own pond (Table IVa). Moreover, in the preponderance of cases, and especially during the peak of the breeding season, they returned in a nearly direct route, and with dispatch, to their nests. On the other hand, those fish which were displaced to an adjacent pond (Fig. 1) were not motivated to move directionally, but swam "aimlessly" (Table IVb).

Table IVa. Return of male green sunfish after daytime displacement within a pond*

Date	Number released	Return Time in minutes
Capture site: N. shore, Pond 2; displaced to S. shore, Pond 2,		
15 June	7	5-11
18 June	15	5-19
	2	45-60
	1	lost float
26 June	5	10-17
	1	lost float
13 July	5	8-30
	1	lost float
Capture site: Pond 1, W. shore; displaced to S. shore		
22 June	4 repeats	4- 5
	3 new	4- 5
Capture site: Pond 1, W. shore; displaced to N. shore		
22 June	3 repeats	4- 5
	3 new	4- 5

*At no time was the sun completely invisible.

Table IVb. Movement of male green sunfish after daytime displacement to a strange pond*

Date	Number released	Results
Capture site: S. shore, Pond 2; displaced to S. shore, Pond 1		
15 June	2	"aimless" wandering
	1	lost
Capture site: S. shore, Pond 1; displaced to N. shore, Pond 2		
26 June	3	none moved
Capture site: S. shore, Pond 1; displaced to S. shore, Pond 2		
26 June	3	"aimless" wandering
Capture site: N. shore, Pond 1; displaced to S. shore, Pond 2		
13 July	2	"aimless" wandering
	3	lost floats

*At no time was the sun completely invisible.

Largemouth Bass

An attempt was made, as with the green sunfish, to trace the return paths of largemouth black bass by means of buoys which were affixed to the posterior portion of the musculature of the dorsal fin with a long thread of monofilament nylon. Unfortunately, this attempt was made rather late in the summer, during a time when our netting records indicated that return to the capture-site is not as precise as during the weeks of early- and mid-summer. The results, although inconclusive, were sufficiently promising to inspire plans for another attempt during the summer of 1957. It was noticed that the best results were obtained from the larger fish. It is possible that a large fish would be better able to tow the buoy without becoming fatigued before reaching its destination. Also, it is conceivable that, with a finite number of territories available in a lake, a large fish might be better able to capture and defend such a territory than would a small one. If this were the case, the smaller fish might not have a firmly established territory, if, indeed, it had one at all.

Soon after these operations were started, it became apparent that some of the fish became fatigued and, consequently, stopped before any shoreline was reached. If, in these cases, the attached monofilament nylon line were so long as to permit the fish to hang down into the hypolimnion, the fish, deprived of its oxygen supply, soon asphyxiated. It was found, upon inspection of the data, that most of these fish had been caught by hook and line and that those which had been captured in a fyke net did not have this difficulty. The struggle which the hooked fish produced apparently caused a condition of fatigue (Black 1955) which, owing perhaps to an inefficient circulatory system, the fish was not able to overcome before it had reached shallow water.

SIGNIFICANCE

It must be kept in mind, in evaluating the performance of these fishes, that they are untrained and undomesticated animals. Hence, if they are displaced, their behavior may not be comparable to the "return to a loft" behavior which is found in trained pigeons. It may be possible, however, that fishes could be selectively bred, and trained, to return to a "home" area, as has been done with domesticated pigeons.

The mechanisms, or stimuli, used by these fishes in orienting toward, and returning to, the area in which they had been captured are, as yet, not fully explained. It is possible that the green sunfish, in their shallow ponds, used local landmarks, as does the fish *Bathygobius soporator* (Aronson 1951), to the exclusion of other stimuli, while the largemouth bass were probably unable to do so, owing to the fact that the waters of Riley Lake and Farm Pond one are deeply stained, and light penetration is greatly reduced. This fact, coupled with the depth at the release point, renders unlikely the use of bottom contours as an immediate guide. Furthermore, these fish were too far from shore to utilize the treeline as a mark. The shore, if visible at all in the fish's "window" (See Fig. 129, p. 378 in Walls, 1942), is most certainly a confused irregular picture, greatly decreased in size. With a slight wind, and hence a rough surface, the edge of this circle would be a constantly changing micro-image of the shore.

It is rather obvious that a searching process should not be ruled out completely. From our recent studies (Hasler *et al.,* 1958), however, it seems clear that some fishes (bluegill, pumpkinseeds, and white bass) have a "sun-compass" mechanism similar to that found in homing pigeons and starlings by Kramer (1952). If this mechanism is present why then were the green sunfish so disoriented when transferred from one pond (Pond 2) to another (Pond 1) nearby (Fig. 1)? The absence of familiar reference points, the presence of strange odors, or numerous other factors may be affecting these transplanted fishes. Further experimentation will be necesary to explain their behavior.

Random movement of marked fish, or of netting effort, is a requirement for applying most mark-and-recapture methods to estimate the number of individuals in a bass population. It is clear from our data that the movement of these fish in summer is not random and, if an adequate program of random netting is not utilized, an estimate from non-corrected data will be an erroneous one. Our studies of bass populations in lakes of up to 80 acres in area, in early spring and in autumn convince us, however, that random movement often occurs at these times and that more reliable estimates can be made by proper methods in these seasons.

Factors which might influence the accuracy of homing include:

1. Sex. This study did not attempt to establish the degree of faithfulness of homing in the sexes. A differential ability may exist.
2. Number of territories. Only a very limited number of territories may be available and, in addition, all males may not be equally capable of occupying and defending one. Hence, if non-territory males are displaced, the motivation for return may not be as great.
3. Age. While our data suggest little difference in the homing ability of fish of different ages, it is possible that there is an age-related factor in homing.
4. Landmarks in pond or lake. It is evident from the data obtained that the green sunfish returned to the site of their original capture with a greater degree of accuracy than did the largemouth bass. It is possible that this difference was due to the absence of landmarks within the body of water in the case of the largemouth bass, whereas the green sunfish had a variety of landmarks available.
5. Season. It became evident, during these studies, that the accuracy of return to the site of capture

varied with the season, being greater during the weeks of midsummer than in spring or in fall. 6. Distance displaced. It is possible that a fish could be displaced to a point so far from its "home" area that it would be unable to return, as sometimes happens even with trained pigeons. This possibility is, of course, dependent both on the size of the lake or pond, and on the "homing" tendencies of the individuals involved.

SUMMARY

Data have been presented which show that displaced green sunfish and largemouth bass return to the site of their original capture, but with varying degrees of success. It is suggested that such things as sex of the individual, number of available territories in the lake or pond, age of the individual, presence or absence of landmarks within the lake or pond, and season of the year could affect the speed and accuracy of return of a displaced fish.

Individual green sunfish in a shallow pond appear to return, in the spring, to the same area occupied the previous summer. Furthermore, it was shown by direct observation of buoyed fish that their return path, after release, is direct and does not include movements that could be described as wandering or random in nature.

Displaced largemouth bass did not return to their capture-area with the same precision as that seen in the green sunfish. It is postulated that this might be partly due to the lack of easily-visible landmarks within the waters of the deeper, rather dark, lakes in which these experiments were conducted, as well as to the longer distances which they had to traverse. It was found, however, that, like the green sunfish, they had maintained their position in the lakes from one summer to another in spite of the intervening winter.

Owing to the non-random behavior of these fish during the summer months, it is suggested that population estimates made during these weeks should be of a design which does not require an assumption of random movement of the members of the population.

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SPATIAL AND POPULATION RELATIONSHIPS BETWEEN *MICROTUS* AND *BLARINA*[1]

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Some of the predatory abilities of the short-tailed shrew (*Blarina brevicauda*) have been recognized for over one hundred years, yet there is little information available concerning the ecological relationships of this aggressive insectivore to other small animals. Eadie (1944, 1948, 1952) has conducted the only substantial investigations aimed directly at the probable effects of *Blarina* on mouse populations. He indicated that meadow mice (*Microtus pennsylvanicus*) formed a large part of the diet of certain shrews during the winter months in field habitats. A relatively stable, high population of *Blarina* in his Ithaca, New York, study areas may have been responsible for the failure of the local *Microtus* populations to reach a peak over a six-year period. A better understanding of this predator-prey relationship is essential to an understanding of the dynamic population patterns of the economically important meadow mouse. The purpose of this paper is to describe the findings of two different approaches to the basic problem of how the two protagonists make mutual use of space, and to formulate a probable pattern of population relationships for the shrew and the mouse.

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Areas and Methods

These studies were conducted on abandoned farm land near Ithaca (Tompkins County), New York from the spring of 1952 to the fall of 1954. Four general regions were selected for study. The Arnot Forest, 17 miles southwest of Ithaca, and Connecticut Hill, 14 miles west of Ithaca, represent abandoned hill-top farms, formerly in hay and pasture; the East Hill Airport area, 5 miles northeast of Ithaca, represents flat, poorly drained field habitats, formerly in forage and cultivation; and the Inlet Valley, one mile west of Ithaca, is an alluvial flood plain, formerly in pasture.

Eleven fields were selected for extensive study in these areas. Following the census methods of Calhoun (1948), permanent lines of stakes, numbered from one through twenty and spaced 50 feet (15.3 m) apart, were set in straight lines through the fields. Two such lines, parallel and about 200 feet (61 m) apart were established in all but the following fields: *Arnot 4* consisted of but a single line, *Arnot 5* had 30 stations in each of its two lines, and the lines of *Connecticut Hill 3* diverged at a 45° angle. Three mouse-size snap-traps were baited with peanut butter, set within five feet (1.5 m) of each stake, and checked for three consecutive days during each census period. Rebaiting was done with a pinch of rolled oats when the peanut butter was removed by invertebrates, but, since most traps were carefully set across runways or near burrows, the baiting was considered of little importance to the capture of *Microtus* and *Blarina*. Each captured animal was tagged with the date and location. The census periods included the summer (July to mid-September) of 1952 and the springs (mid-March through April) and late summers (mid-August to mid-September) of the next two years.

An intensive study was conducted in the Airport region during the summer of 1954. This 12-acre (4.9 ha) area included two acres (0.8 ha) that had been planted to corn in 1951, and the rest was long-abandoned pasture. Much of the area was poorly drained with a slope of less than 1 percent. The old-fields bore a fairly dense, but not uniform cover of Canada bluegrass (*Poa compressa*) in the better drained portions, and redtop (*Agrostis alba*) in the poorer drained portions. Lance-leaved goldenrod (*Solidago graminifolia*) was a conspicuous associate in 1954. The better drained portions of the pasture varied from a good timothy (*Phleum pratense*)-goldenrod cover to sparse strawberry (*Fragaria*)-hawkweed (*Hieracium*)-cinquefoil (*Potentilla*) cover. The poorly drained portions provided, for the most part, a dense cover of sedges (*Carex* spp.), wool-grass (*Scirpus cyparinus*), various grasses, and sensitive fern (*Onoclea sensibilis*), with asters (*Aster* spp.) and clumps of willows (*Salix* spp.) abundant. Much of the poorly drained area held standing water from November until May. Half of this area was bordered by mown timothy hay, a road, and dry woods, and half by habitat similar to the internal features (Fig. 1).

A grid of 200 stations, spaced 50 by 50 feet, was established in these 12 acres. Half of a quart-size, paraffin-coated, milk carton was placed on its side with the open end in a runway or other suitable site at each station. A pinch of rolled oats was placed in the back of each carton for bait. These cartons were durable over the summer period and provided excellent protection for their contents from the wind and rain. Each day, for periods of at least 10 consecutive days each in June, July, and August, four days in September, and 5 days in October, the cartons were checked for signs of small mammal activity. The presence of scats (fecal droppings) identifiable as those of *Microtus, Blarina,* or *Sorex cinereus,* and the removal of bait without defecation were recorded. *Sorex* scats were distinguished from those of *Blarina* on the basis of size, and scats classed as intermediate in size were re-evaluated after a comparison with more certain records from the same stations on other days. A negligible number of *Microsorex hoyi* were present in the area, but their scats cannot be distinguished from these of *Sorex cinereus*. During the summer, the area was selectively live-trapped to catch *Microtus* and

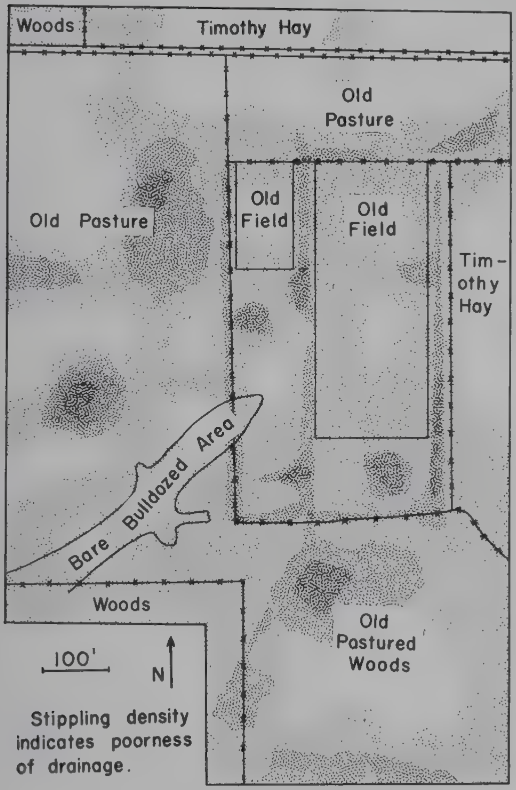

FIG. 1. Map of the intensively studied Airport field. A border of approximately 100 feet surrounds the area covered by the grid of bait stations.

avoid *Blarina,* which is highly susceptible to trap mortality. This was effected by substituting traps for cartons at stations where *Blarina* had not been recorded. When it was desired to trap a station that had been used by both species, the big shrews could be avoided by placing the trap on top of the ground-covering litter and vegetation, instead of in the runway. The mice located the traps readily, while the semi-fossorial shrews did not leave the cover of the litter. Mice were marked by toe-clipping and released promptly at the capture site. At the end of the bait check in September, the area was trapped thoroughly by placing a snap-trap inside each carton for three days and a trap half-way between stations for the next four days. Bait stations were checked again in October and the area retrapped.

RESULTS

The extensive snap-trap censuses yielded more than 1100 *Microtus* and 400 *Blarina,* as well as 390 specimens of 11 other kinds of small mammals. The numbers of *Microtus* and *Blarina* taken in each census are indicated in Table I, without comment as to the variables of weather, bait, and misses that may have influenced the catch. Analyses of these data yielded several observations pertinent to the problem at hand. These are concerned with the fluctuations of the populations, the relative numbers occupying areas, and the spatial relationships of the two common species.

TABLE I. Numbers of *Microtus* (M) and *Blarina* (B) taken in standard census lines

Region	Field	Summer, 1952		Spring, 1953		Autumn, 1953		Spring, 1954		Autumn, 1954	
		M	B	M	B	M	B	M	B	M	B
Arnot Forest	1	16	3	32	1	17	19	17	0	24	12
	2	9	6	19	0	21	10	9	1	33	7
	3	2	1	5	0	16	4	2	0	31	3
	4	5	2	0	0	1	0	2	1	15	7
	5	12	0	12	1	38	3	16	2	39	5
Connecticut Hill	1	54	11	11	0	15	16	9	0	1	7
	2	36	11	15	2	29	15	1	0	11	12
	3	16	7	12	1	16	15	13	0	3	4
Airport	1	13	5	37	1	30	30	23	0	3	4
	2	27	29	37	5	62	24	22	1	22	20
Inlet Valley	1	31	36	50	3	79	38	38	3	19	21
Total...	11	219	111	230	14	324	174	152	8	201	102

The relative population fluctuations of the two species have been graphed in Figure 2. The numbers taken in the individual fields have been combined and averaged by regions for convenience, with the Airport and Valley populations combined because of their great similarities. This procedure does not imply that the regions should necessarily be treated as single populations. In detailed population studies, even single fields should be tested for homogeniety. The overall patterns are so similar in this instance that no greater detail is warranted.

All populations of *Blarina* behaved similarly. Winter mortality reduced their numbers to about 10 percent of the summer peak. This great mortality is probably confined to open fields that are subjected to sudden freezing and thawing in this region. Professors William J. Hamilton, Jr. and W. Robert Eadie have not observed such a great general decline over winter in many years of trapping in the Ithaca region. Micro-climatic differences between fields and woods are well known (Spaeth and Diebold, 1938), and Pruitt (1953) has suggested that similar differences between forest types may control the local distribution of *Blarina* in Michigan. The semi-fossorial habits of the shrew account for its vulnerability to sudden changes in soil moisture and temperature. *Microtus* builds its nests and forages above

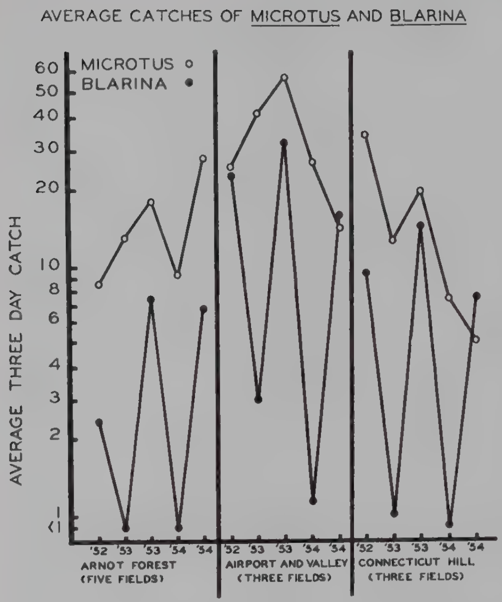

Fig. 2. Relative fluctations of *Microtus* and *Blarina* populations. The numbers are based on snap-trap censuses conducted during the periods of July to mid-September, 1952 and the springs and late summers of 1953 and 1954.

ground during the winter. Probably the presence of hedgerows is of considerable importance to the survival of field-dwelling *Blarina* in the winter. In all regions, the summer of 1953 was somewhat more productive than usual for this shrew.

The *Microtus* populations behaved quite differently in the three regions. Populations at Connecticut Hill were highest in 1952 and extremely low in 1954. The Airport and Valley populations were highest in 1953, and the sparse vegetation of the Arnot fields was ravaged by the voles in 1954. Even within the general regions, some populations could be found that were out of phase with neighboring populations. The intensively studied Airport field and the Fisher field (which will be discussed later) are examples of this.

The fact that some spring censuses indicated a higher population density than did the census of the preceding late summer is due to the breeding activities of the voles after the August-September period. Although breeding usually ceases by November, in some years the mice breed throughout the winter (Hamilton, 1937). Spring trapping in the present study disclosed no juveniles that would indicate the survival of any mice that may have been born in late winter. Although it is possible that high shrew populations of *Arnot 1, Airport 1,* and *Connecticut Hill 3* may have suppressed vole peaks in 1953, still greater populations of shrews apparently failed to reduce peaks in *Airport 2* and *Inlet Valley* the same year. These data strongly suggest an absence of causal interaction in the population fluctuations of the two species.

Some areas supported large numbers of both species in the fall. In several cases (e.g. *Inlet Valley* and *Airport 2,* 1952), the potential predator seemed to outnumber its vertebrate prey. This situation was partly a result of differential responses of the two species to the census method. Figure 3 helps to clarify the situation. It is based on 1059 *Microtus* and 401 *Blarina* from 39 censuses that were not seriously affected by weather conditions. This method is essentially that used by Hayne (1949) and Calhoun (1950, 1951, 1956) to estimate the number of individuals exposed to a trap line by fitting a line to the progressive decline in catch for a three-day period. Percent is used in this figure to equalize the numbers of the two species. Beer, *et al* (1954) suggest that differences in slope indicate the relative trappability of different species. The steeper slope of the *Blarina* line suggests that this species is more trappable than *Microtus,* and the better fit suggests uniformity in its habits and response to

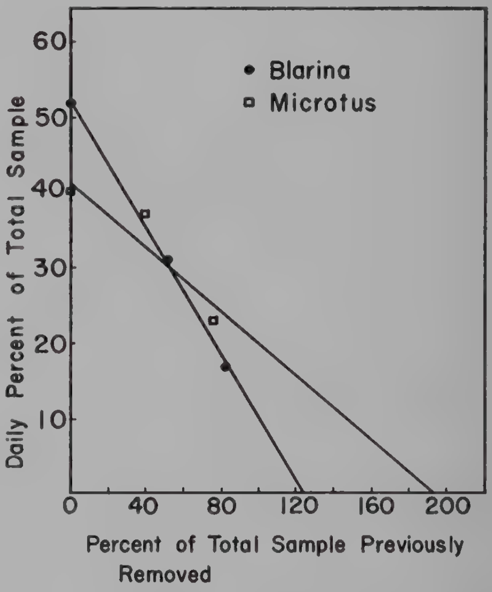

Fig. 3. Estimates of the relative numbers of *Microtus* and *Blarina* exposed to trap lines, based on the numbers caught in three days of trapping.

runway traps. The poor fit of the *Microtus* line suggests variability in its behavior, and, therefore, considerable error may be involved in using this method as a population estimate for the vole. No doubt many factors influence the probability of capture for various species of mammals. The slopes of the lines also vary with the population densities for both species, but the differences due to density are much less than the differences due to species. Since an estimated 81 percent (100/124) of the exposed *Blarina* but only 52 percent (100/193) of the exposed *Microtus* were taken in the census lines, a crude factor of 1.6 may be used to decrease the apparent shrew-vole ratios obtainable from Table I. Thus, for the Valley in 1952, the apparent ratio of 1.2 to 1 (36 shrews to 31 mice) is more likely to be 0.75 to 1. This is still a high ratio of predator to prey, and causes one to wonder how the voles can exist and apparently thrive under such circumstances. Differential use of the micro-habitat affords a possible explanation and stimulated the following analysis.

Following Calhoun's (1951) suggestions, a test for association between *Microtus* and *Blarina* was made for each census by means of a four-fold table and χ^2 test of significance. This measures whether the two species are taken at the same trapping station with greater or less frequency than would be expected by chance alone. In only one case did the test indicate a statistically significant deviation from a random distribution. The census lines of *Connecticut Hill 2* extended from a moist swale across a hill of nearly pure poverty grass (*Danthonia spicata*). Nearly all of the small mammals were taken in the 13 swale stations, thus suggesting a high association. Dice (1952) has indicated the need for a uniform habitat in this type of analysis. In this case, it is obvious that the extremes of vegetation and soil moisture were the factors responsible for the apparent positive association between the shrew and the vole. If the stations from the dry poverty grass are excluded from the calculation, the measured association becomes negligible. Based on snap-trap censuses, the hypothesis of a habitat separation of the two species must be rejected.

Observations on the deposition of scats and the removal of bait at the bait stations in the Airport field provided information on the seasonal changes in the activity of the small mammals, differences in habitat preferences, and measures of interaction between *Microtus* and *Blarina*. Proper interpretations of these data are seriously hampered by a lack of knowledge of small mammal behavior and the role of the bait station in the spatial and social organization of the small mammal community. It should be apparent that this attempt to use a new technique shows much promise but leaves much room for improvement. The greatest advantage in the technique as suggested by Eadie (1948), is that it provides a relative census with a minimum of disturbance to the population.

Some observations on the behavior of three species that used the bait stations may help in interpreting the results. Others (*e.g.*, Fitch, 1954) have observed a lag in acceptance of live-traps by *Microtus* (*M. ochrogaster* in his case), and a negative reaction to new objects is well known in Norway rats (*Rattus norwegicus*) (Chitty, 1954). A similar result was obtained with the bait boxes. A period of 9 days followed the placement of the boxes before the progressive increase in daily utilization by *Microtus* leveled-off. Acceptance of the rolled-oat food source by the two shrew species was much more rapid, although they seemed more variable than *Microtus* in the numbers of stations visited daily (Table II). Analyses were based on observations recorded after the leveling-off stage.

TABLE II. Statistics from 200 bait stations recording *Microtus*, *Blarina*, or *Sorex* scats or bait removal without defecation

	Microtus					*Blarina*				
	June	July	Aug.	Sept.	Oct.	June	July	Aug.	Sept.	Oct.
No. days to stability	9	4	2	2	2	3	3	1	1	2
Mean no. stations visited daily	118.0	112.5	83.4	86.5	32.5	26.7	52.1	73.3	98.0	46.2
Standard error of the mean	4.0	2.7	2.0	1.9	4.7	1.3	2.2	4.2	3.2	6.6
Coefficient of variation, %	6.8	7.2	6.8	4.2	28.9	14.6	13.6	17.3	5.7	28.5
	Sorex					Removal only				
No. days to stability	4	1	1	1	1	3	2	1	1	3
Mean no. stations visited daily	10.9	21.7	47.3	70.0	59.2	70.8	49.3	44.0	23.5	6.3
Standard error of the mean	1.2	1.2	3.8	3.0	5.4	3.7	2.5	2.8	1.6	0.9
Coefficient of variation, %	34.8	18.0	23.8	6.0	20.6	15.8	16.6	18.9	9.3	25.4

The stations, once established and accepted, appear to enter into the daily routine of many of the small mammals and possibly become focal points for spatial organization. The intensive snap-trapping at the end of the summer indicated that the largest (but not necessarily the oldest) and presumably socially dominant male *Microtus* had been marked and later retrapped at the bait stations more readily than had the smaller mice.

The bait does not remain as the primary reason for approach and defecation at stations by some individuals. In August, after the stations had been unbaited for 21 days, they were checked for two consecutive days without rebaiting. The results suggested that the unbaited stations were used about 45 percent as much as baited ones by *Microtus,* 30 percent by *Blarina,* and less than 10 percent by *Sorex*. *Sorex* and *Blarina* frequently defecated on the bait while *Microtus* usually consumed all of the bait before defecating. On several occasions it was observed that bait had been removed from certain stations shortly after they had been rebaited. *Microtus* scats were often deposited later. It was commonly observed that *Microtus* would place a single fecal pellet on a heap of *Blarina* dung. *Sorex* also exhibited this interesting behavior, coincidentally causing many *Sorex* scats to go unobserved. Certainly, defecation is not performed solely for simple physiological reasons by these small mammals.

Reference to Table II shows that the August period registered a marked drop in *Microtus* activity. This 25 percent depression of activity was also evident in the live-trap data for the period. In June and July, a mean of approximately 1.2 mice were caught per station trapped. In August, the mean was only 0.8. In all three periods, individuals were trapped an average of 2.2 times each. This suggests a drop in either population level or in trapability of 33 percent.

In search of an explanation for this decline, shrew predation was suspected. Of 70 *Blarina* scats collected throughout the summer, however, none contained mouse hair. This would tend to exonerate the shrews. Another observation suggested that the decline might be explained by a change in behavior, rather than by a change in numbers. During June and July more than half of the stations visited by *Microtus* had fecal pellets placed on top of the carton as well as in it. In August and September, considerably less than half of the used stations had scats placed on top. Possibly this change was related to an increase in social stress, but it could just as well have been due to the weather. In nature, the mice often utilize stones in dry fields or tussocks in wet fields for the deposition of feces. Perhaps these sites act as scent posts for marking territories or attracting members of the opposite sex. Too little is known of the ethological role of scat placement to justify a hypothesis. In contrast to *Microtus* the shrews were known to defecate on top of the cartons in only one instance for each species.

Whether the decline in *Microtus* activity at the bait stations actually represents a population change cannot be said with much certainty. The increase in measured activity of the two shrew populations seems quite in agreement with known life history data and is the first time to the author's knowledge that any measurement of the natural rate of increase in a wild shrew population has been made. Actually, the seasonal differences in rate of bait station use for any of the three species is not an accurate reflection of the relative population changes even if behavior remains constant. This is because one animal may use several stations, and several animals may use the same station. Thus, in September, approximately 2.1 stations were in use for each *Blarina* snap-trapped (98 stations for 47 *Blarina*). In October, there were 2.9 (46/16) stations in use per *Blarina* trapped. The same sort of relations were true for *Microtus* and *Sorex*. High populations will be underestimated and low populations overestimated when simple presence-or-absence of scats is used as the criterion. Tevis (1956), using percent of seed spots robbed by small mammals, also concluded that his method did not provide exact figures on population density.

Again, as with the snap-trap census, it is obvious that different species cannot be compared directly. While the *Blarina* were using 2.1 and 2.9 stations per individual in September and October, respectively, *Microtus* was using an average of only 0.7 and 1.6 stations per mouse trapped. This difference seems to be a reflection of the greater metabolism, activity, and home range of the shrew; possibly the measurement of activity is better for some ecological comparisions than is the number of individuals. A more reliable census could be developed with more detailed quantitative estimates of the scats present at each station.

The spatial distribution of activity, as measured by the bait stations, was not random with regard to habitat. Gross differences in the microhabitats of this area were obvious. Floristics and litter cover varied greatly with the changes in soil drainage and past history of utilization but were not readily mapped to good effect. Blending of types and smallness of units relative to the home ranges of the animals and to the spacing of the stations were the major deterrents. The recently cultivated fields, on the other hand, were well defined by the plow and were reasonably homogeneous with regard to the very low litter density and the low average vegetative cover.

Thirty-three of the 200 stations occurred in these old-field areas. Comparing this habitat with all others gave the significant differences in small mammal activity which are summarized in Table III. *Microtus* showed a preference for the old-fields in July but avoided them in September. This observation should not be looked on as evidence for movements of *Microtus* from one area

TABLE III. A comparison of small mammal activity at 33 old-field stations with 167 other stations

	June	July	Aug.	Sept.	Oct.
Microtus	0	+	0	− −	− −
Blarina	− −	− −	− −	− −	− −
Sorex	−	0	++	0	−
Bait removal only	− −	0	++	++	−

+ and ++ indicate positive association at the 5% and 1% levels of significance.
0 indicates no significant deviation from a random distribution.
− and − − indicate negative association at the 5% and 1% levels of significance.

to another, as suggested by Hamilton (1941) and Linduska (1950) (based on snap trapping). The data probably indicate a shifting of centers of activity, since the areas involved were quite small in relation to normal home ranges, and since no marked adult mice were known to have moved unusual distances during the study. Blair (1940) cites the movement of two marked mice from upland to lowland habitats, but apparently these distances were relatively short. Also, *Sorex* activities in the old-fields reached a peak in August and *Blarina* indicated a strong avoidance of these areas in all months. The October determinations are not valid because these old-field areas were too far removed from sources of re-invasion (Fig. 1) following the September snap-trapping. It is probable that a proper evaluation of bait removal without defecation could alter the picture for *Microtus* and *Sorex* somewhat. Such an evaluation would also improve the value of the method for census purposes. Since a distinction in seasonal habitat preferences by the various species can be demonstrated in this well defined habitat, it is likely that similar quantitative relationships exist in other facies of the total area. These might be determined by use of a more closely spaced grid of stations and more detailed mapping.

Some indication of the factors limiting the micro-distribution of these animals may be obtained by listing the factors associated with stations that were used but little, or were completely unused during the entire summer. Of 40 stations visited less than three times by *Blarina,* 18 were in the old-fields and 11 were in the dry *Fragaria-Hieracium-Potentilla* association. Of 11 stations used less than four times by *Microtus,* 8 were active *Blarina* stations. All of the preferred *Blarina* habitat appeared to be favorable *Microtus* habitat, and the failure of the stations in question to be used by the vole seems to indicate an active effect by the large shrew. Possibly these 8 stations were located near the nests of *Blarina,* since many other stations in equally active use by the shrew were also used by *Microtus.*

The measurement of interspecific association between *Microtus* and *Blarina* was the primary aim of this study. The formulae recommended by Cole (1949) were used to obtain the coefficients of association presented in Table IV. For the first three periods and October, stations recording fewer than three days of use were arbitrarily designated as inactive for the species in question. A record of two days of use was the lower limit of activity used in September. Juggling this arbitrary level of separation or using a finer division in the degree of activity does not change the aspect of the general picture, but does, of course, alter the statistics somewhat.

TABLE IV. Measurements of association between *Microtus* and *Blarina* based on the frequency of joint use of 200 bait stations

	NUMBERS OF STATIONS				
	June	July	Aug.	Sept.	Oct.
Microtus only	96	114	53	28	17
Blarina only	19	27	47	61	24
Both active	15	41	59	60	12
Neither active	70	18	41	51	147
Coef. association	−0.21	−0.39	−0.00	+0.13	+0.22
Chi square	2.1	17.5†	0.01	3.9*	12.6†

*Significant at the 5% level. †Significant at the 1% level.

It was determined that a change in association occurred, going from significantly negative in early summer to significantly positive in late summer. This change is related to two things: the progressive expansion of the areas used by the increasing shrew population and the change in habitat preference indicated by the voles. Apparently the effects of summer dryness on the soil and vegetation caused the voles to become more active in the moister areas preferred by the big shrews. The presence of *Blarina* is more acceptable to *Microtus* than is a severe inanimate environment. The positive association measured in October is partly due to simultaneous invasion of the trapped-out area from the same direction by both species and to the inclusion of large, uninvaded areas in the calculations.

Daily calculations give a slightly different picture of the association in September. Although the combined data indicate a positive association, the simultaneous occurrence of the scats of the two species did not deviate from randomness. Positive association, then, was caused by the alternate use of many stations by the two species. It should be realized that daily observations imply no more close temporal relationships than the summaries for the periods, since a gap of as much as 24 hours may occur between the "simultaneous" defecations, while scats observed on successive days may have been deposited minutes apart.

In order to determine whether the expanding shrew population was actively driving the mice from occupied range, the following analysis was used. For each period, each station was assigned a number from 0 to 3 according to the frequency of observed *Microtus* scats. Similarly, a second number was assigned for *Blarina*. Using only those stations that had been assigned either ones or twos during the previous period (and were therefore free to fluctuate either up or down), the changes in activity between adjacent periods were determined for each station by species. These data were then entered in a four-fold table, which then indicated at how many stations the activities of both species had increased, both deceased, or one increased while the other decreased. A χ^2 value of 5.7 suggested a significant negative correlation in the activity fluctuations between June and July. Fisher's (1941) exact method, however, gives a probability of 0.063, a value slightly greater than that usually accepted as being significant. Considering the poorness of the June analysis resulting from the lag in the acceptance of the stations by *Microtus,* it is better to accept the hypothesis of randomness in the shifts of station activity. Station changes between July and August were quite random between the two species, and it must be concluded that the expanding *Blarina* population did not cause a reduction in the areas of *Microtus* activity.

The above studies would not be complete without an attempt to assess the validity of using bait stations in measuring the distribution and activity of the various species. Such an evaluation of methods was obtained by comparing the animals snap-trapped at stations in September with activity estimates made immediately prior to the trapping. Stations were designated as active (*A*), intermediate (*I*), or inactive (*O*) for each species. Because there were no differences in the results between *A* and *I* stations for *Microtus* and *Sorex,* or between *I* and *O* stations for *Blarina*, these groups were combined in the following results:

22 percent of 112 *A* stations took 88 percent of the *Blarina* catch, or 0.3/station.

6 percent of 88 *I* and *O* stations took 12 percent of the *Blarina* catch, or 0.06/station.

64 percent of 127 *A* and *I* stations took 77 percent of the *Microtus,* or 0.9/station.

41 percent of 73 *O* stations took 23 percent of the *Microtus* catch, or 0.5/station.

32 percent of 104 *A* and *I* stations took 59 percent of the *Sorex,* or 0.4/station.

23 percent of 96 *O* stations took 41 percent of the *Sorex* catch, or 0.3/station.

Based on the original data (rather than on the percentages listed above), all differences observed for the *Blarina* were significant at the 1 percent level, all differences for *Microtus* were significant at the 5 percent level, and none of the *Sorex* differences were statistically significant. Thus, the correlation between the two methods for recording activity and distribution is excellent for *Blarina,* satisfactory for *Microtus,* and poor for *Sorex.*

In defense of the results, it should be indicated that the necessarily short check of bait stations in September was not entirely adequate to establish activity levels, and it is not now possible to predict the effects of removal trapping on the movements of individuals in the disturbed population. In the case of *Sorex,* its capture depends on the distribution of very sensitive traps. It was revealing to find the scats of this species deposited on the treadles of unsprung traps.

The above snap-trapping results also suggested that the survival of young *Microtus* had become exceptionally low in this area. Exactly what "normal" survival can be expected is not easily calculated; however, the mice in the Fisher field, about four miles away, provide a reasonable comparison. This field, which also had been live-trapped during the summer of 1954, was thoroughly snap-trapped immediately following the snap-trapping at the Airport field. The Fisher field produced a population of 60 mice on a single acre (0.41 ha), which must have been near a peak, while the Airport field supported an average of only 15 mice per acre, probably a high population for the mixed habitat.

Table V compares the number of young mice snap-trapped on each area with the number of breeding females. The ratios of visibly pregnant females to visibly non-pregnant adults is identical in the two areas—2.2 to 1. The average number of embryos is not significantly different, statistically, although the Airport field has a slightly higher mean. Using live-trap observations, as a basis, no interruptions of breeding occurred on either field during the summer. With the evidence at hand, it seems reasonable to assume that the breeding rates were nearly identical in the two fields during the late summer.

Using the numbers of pregnant females as a basis for comparison, an analysis of the table indicates that the survival of young weighing more than 15 grams when trapped was equal in the

TABLE V. A comparison of the *Microtus* populations snap-trapped on the Fisher and Airport fields on September, 1954

	Fisher	Airport
Acreage	1	12
Total population size	62	179
Number of non-pregnant adults	6	19
Number visibly pregnant	13	42
Average number of embryos	4.2	4.5
No. of mice weighing 5 to 10 gms.	5	0
" 11 to 15 gms.	4	4
" 16 to 20 gms.	4	18
" 21 to 25 gms.	18	47
Total number of 25 grams or less	31	69

two areas. The high number of mice in the largest weight class is somewhat misleading, since growth is often arrested at this pre-pubertal stage in late summer (Barbehenn, 1955) causing a greater spread in the age of this group. The difference between areas in the number of mice weighing 15 grams or less is statistically highly significant. Only half as many were trapped at the Airport which should have produced three times as many as the Fisher field. Obviously, survival was low in both fields.

DISCUSSION

The fragmentary evidence provided by the snap-trap censuses suggest no causal relationship between the fluctuations of *Microtus* and *Blarina* populations and implies no ecological interaction. Bodenheimer (1949) arrived at this same conclusion by studying the ratios of *Microtus guentheri* and the shrew, *Crocidura russala,* in owl pellets in Palestine. In the light of Eadie's observations, however, this implication is hard to justify. These data suffer from several serious weaknesses. Foremost of these is the lack of continuity between censuses. Six months is a long time to ignore the events in rapidly changing populations, and any attempt to reconstruct the middle from the ends cannot be very convincing. Also, in the measurement of interspecific association from snap-trap results, it is apparent that differential responses to the traps exist between species, and it is probable that any community organization that may have existed prior to trapping is destroyed with the first night's catch. One would expect randomness to result.

The results indicating excessive loss of young at the Airport field are not easily explained. The two most likely causes for the differences in survival between the two fields are internal population stresses and shrew predation. All too little is known of the mechanisms involved in the first suggested cause, although considerable research and thought have been stimulated by Christian's (1950) original application of Selye's (1946) principles to wild populations. High mortality among juveniles is a reality in captive populations of various species (*e.g.* Southwick, 1955 and Christian, 1956 for *Mus musculus;* Clarke, 1955, for *Microtus agrestis;* Louch, 1956, for *M. pennsylvanicus*), but natural populations have not been studied with sufficient detail to enable one to predict the effects of various population densities. Chitty (1952) and Godfrey (1955) found losses of juvenile *M. agrestis* to be highest in litters born early in the breeding season of peak years. If population stresses are responsible for the differences observed in the present study it would appear more logical that the much denser population of the Fisher field would have suffered the most. Since this was not the case, the intraspecific stress hypothesis is not a satisfactory explanation for the difference in survival of young.

The biggest apparent difference between these two vertebrate communities was in the numbers of shrews. No *Sorex* were present in the Fisher field and the few *Blarina* that wandered in from the adjacent woods were systematically removed by live-trapping. Mice, weighing less than 16 grams when trapped, were probably born about mid-August or later. The drop in survival rate therefore coincided with the development of positive association between the shrew and the vole. Judging by the readiness with which *Blarina* finds bait boxes placed in runways, it would seem inevitable that they would locate the majority of the mouse nests in an area where both species occur. Possibly a nursing mouse can repel the average shrew that is not pressed by hunger, but unguarded nestlings and weanlings would seem certain to be destroyed. Evidence of this would be very difficult to obtain in the field. Shrew scats would contain little hair from relatively naked young, and a low rate of nest predation per shrew might be significant to the mouse population. If pregnancy rates remained the same at the Airport field, approximately 10 young per day might be born in the area. Divided among some 40 *Blarina,* and possibly a hundred *Sorex,* this number of small mice would not contribute greatly to the total amount of food consumed by the shrews, even if the shrews were the sole cause of complete mortality. It also may be that an increased rate of shrew-mouse contacts adds to the stress resulting from intraspecific contacts.

In fairness, it should be repeated that a change in behavior may have been responsible for the July-August decline in *Microtus* activity at the Airport. If this was the case, it may have been at-tended by a change in survival rate. Activity measurements were not made at the Fisher field so no comparison is possible. The shrews, possibly both species, remain as the most probable cause of the excessive loss of young in the *Microtus* population at the Airport field during the August-September period.

Despite weaknesses in collecting and interpreting these data, a dynamic picture of population interaction between *Microtus* and *Blarina* can be hypothesized as follows:

Normal winters in the Ithaca region cause a great reduction in open-field *Blarina* populations prior to the commencement of spring breeding for either species. This permits the *Microtus* population to expand freely if other factors are suitable. By mid-summer, shrew populations in suitable fields have increased greatly as a result of immigration from woodlands and reproduction in the fields. Low soil moisture and associated vegetational changes brought about by summer dryness cause the mice to make greater use of the moister areas preferred by the large shrews. This establishes a situation that gives maximum exposure of mouse nests and individuals to shrew predation and survival of young mice becomes increasingly lower.

The significance to the mouse population of this predation on young must vary with the particular circumstances. If the mouse population had begun the spring season with a moderate level of abundance and had reproduced successfully, internal stress mechanisms might be more important in limiting further reproduction and population growth than the shrews. A high fall population of shrews could contribute to the formation of an old-age *Microtus* population going into the winter. On the other hand, if *Blarina* is capable of retarding the population growth of the mice before density dependent stress develops, it may be an asset to the mouse population, since the surviving young would be more "normal" (*sensu* Chitty, 1952).

If Eadie's observations are generally applicable, the time and rate at which the *Blarina* population declines in the winter must be of considerable importance to the *Microtus* population. In his work, it appeared that *Blarina* maintained relatively high over-wintering levels, and the voles failed to generate a high population over a six-year period. The peculiarities of weather and habitat interspersion are very important in the relationships of the populations.

It is unlikely that two organisms with one-year life spans and different life history patterns should follow any particular related sequence of population fluctuations. The situation does not resemble the cycle of the lynx, which is dependent on that of the snowshoe hare (Elton and Nicholson, 1942). *Blarina* is not dependent on *Microtus* for food in the summer, and many *Blarina* seem destined to perish in the winter anyhow. The relatively regular, high annual turnover in open-field *Blarina* populations should be relatively independent of the fluctuations of the vole populations. Recognizing the seasonal aspects of the shrew predation, it should follow that any effects of the shrews on the vole population must depend largely on the condition of the vole population at the time. Since this varies from year to year no obvious pattern can develop in the relationship. Although *Blarina* bears no apparent causal relationship to the more-or-less regular microtine "cycles," it should not be ruled-out as a potentially important agent which may either dampen and prolong the cycle, or materially aid in establishing an unstable population likely to "crash" over winter. Population relationships are not static between seasons and years, and it is obvious that we need to know much more about population dynamics in simple communities before the details of such complex situations as exist between the vole and the shrew can be determined.

SUMMARY

1. Spatial and population relationships between *Microtus* and *Blarina* were studied with two methods. Five semi-annual, standardized, snap-trap censuses were made on eleven fields in four regions near Ithaca, New York, between the summer of 1952 and the fall of 1954. A grid of 200 bait stations was established in a 12-acre area and the distribution and frequency of mouse and shrew scats were recorded during periods from June through October, 1954. This area was live-trapped during the summer and snap-trapped at the end.

2. *Blarina* populations in open fields undergo a drastic annual turn-over involving high winter mortality. *Microtus* populations appear to fluctuate independently of the *Blarina* populations. The microtine cycles were completely out of phase with each other in three of the four regions and some fields within regions were out of phase with the majority.

3. In the fall, population densities of the two species may be nearly equal in some areas and the snap-trapped individuals are randomly distributed with respect to each other, if the habitat is uniform.

4. The number of bait stations visited daily by *Microtus* declined by 25 percent between July and

August. Stations visited by *Blarina* increased four-fold and those visited by *Sorex* increased seven-fold from June to September. The drop in *Microtus* activity could not be attributed to shrew predation.

5. Using two recently cultivated parts of the area as discrete units of micro-habitat, it was determined that *Blarina* strongly avoided these areas in all months. *Sorex* showed a distinct preference for the areas in August, and *Microtus* activity went from a positive preference in July to negative in September. These preferences were related to conditions of soil moisture and vegetative cover.

6. Coincidental with the change in habitat preference indicated by *Microtus,* the association between *Microtus* and *Blarina* went from negative in July to positive in September. The expanding shrew population did not cause a reduction in the areas used by the mice. An active effect of *Blarina* on the distribution and activity of *Microtus* occurred at eight stations which may have been near den sites of the big shrew.

7. The validity of the bait station results were checked by snap-trapping. Results were excellent for *Blarina,* satisfactory for *Microtus,* and poor for *Sorex.*

8. In comparison with another peak population under study, survival of young *Microtus* in the Airport area was unusually low for mice born after 15 August. Since this was associated with the change to positive association between the mouse and the big shrew, it was inferred that predation on nestlings by the shrews was responsible for the low survival rate of young.

9. A hypothesis for the relationships between the population dynamics of the two species is presented. The consequences of shrew predation on *Microtus* populations depends on the condition of the vole population and the timing of the predation. Since these factors vary with locality, season, and year, no regular pattern of relationships can develop. Presumably, the shrews are capable of either precipitating a decline or prolonging a normal microtine cycle.

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SOME EFFECTS OF THINNING ON A POPULATION OF FISHES[1]

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Introduction

Purpose and scope

Many workers have concluded that the growth of individual members of a fish population is inversely proportional to the density. This is in support of the results of Walter (1934) in his extensive analysis of the factors which influence the growth of carp in ponds, and his efforts were among the earliest that placed fish production on a scientific basis. Church (1927) and Shaw (1929), as cited by Schneberger (1935), studied the effect of crowding on the growth of the tropical fish *Platypoecilus maculatus* and found that the least number of fish per unit of volume grew at the greatest rate.

Ricker and Foerster (1948) report that the average weight of sockeye salmon (*Oncorhynchus nerka*) belonging to year classes with few individuals is higher than that of sockeye of year classes with many individuals. This also has been shown for rainbow trout (*Salmo gairdneri*) in small lakes of northern Wisconsin (Johnson and Hasler 1954).

Bardach (1951), on the basis of historical reports, believed that a severe reduction in numbers was followed by an increase in the average length and weight yellow perch (*Perca flavescens*) in Lake Mendota, Wisconsin. Churchill (1949) was unable to show an increase in rate of growth in length of perch in Curtis Lake, Wisconsin, after netting had removed 69.8 kilograms per hectare over a four-year period; however, the fish were heavier at a given length than before removal. Dymond (1926) and Schneberger (*op. cit.*) state that the perch in Lake Nipigon, Ontario, and Nebish, Silver, and Weber Lakes, Wisconsin attain lengths which are correlated negatively with relative abundance based upon frequency of capture in nets. Eschmeyer (1937, 1938) obtained similar results, as did Alm (1946) who transplanted perch (*Perca fluviatilis*) to non-perch waters. On the other hand, removal of most of the perch in Lake Windermere, England, failed to produce a significant change in rate of growth (LeCren 1949).

In Alabama ponds, the addition of more bluegills (*Lepomis macrochirus*) without increasing the food supply decreased the average size of the fish surviving (Swingle and Smith 1939). Swingle has focused attention on the relationship between production and weight of predator and prey fish. He points out that, in general, a ratio of the weights of forage to carnivorous species of from 3.0 to 6.0 is most desirable (Swingle 1950).

King (1953) described an unsuccessful attempt to increase the growth of fishes in Lake Hiwassee, Oklahoma, by eliminating part of the population with rotenone. One- and two-year old largemouth bass (*Micropterus salmoides*) showed a slight increase, but older fish did not. Shoreline spraying killed many bluegills without affecting the growth of the remainder.

Following reduction of population densities by winterkill, Beckman (1950) observed an increased rate of growth for bluegills, yellow perch, and pumpkinseeds (*Lepomis gibbosus*), and a very small increase for largemouth bass. These advantageous growth rates were sustained for only a few years. Beckman (1941, 1943) previously had reported a marked positive change in the growth rate of rock bass (*Ambloplites rupestris*) after approximately one-half of Standard Lake, Michigan, was poisoned with powdered derris root.

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Two years after the stocking of a new pond with bluegills, over-population from natural spawn caused stunting (Bennett 1943). Stunted breeder bluegills taken from Homewood Lake and placed in Fork Lake, Illinois, grew as much during the succeeding 15 months as they did during the past two to five years (Bennett, Thompson, and Parr 1940). A growth stimulus produced by severe thinning of the bluegill population in Ridge Lake, Illinois, has been noted by Bennett (1954).

In 1952, a study was begun by Johnson, *et al.* (1953) which had as its objective the determination of the effects of removal of excess rough fish and stunted pan fish on the growth and survival of largemouth bass. The work was continued through 1956 by me and was enlarged to include the effects on other species. Many of the early workers performed their thinning experiments in the laboratory or in artificial ponds which could be drained periodically. A need for more quantitative data on the growth-density relationship in small natural lakes is foremost among the reasons which prompted this study. In addition, the varied methods which have been used in the past to analyze growth after a reduction in numbers seem to lack the precision necessary for adequate appraisal, and pre-treatment estimates of the population size often were omitted. Throughout the following discussion of the results of this five-year program emphasis has been placed on the application of a consistent, analytical approach.

Description of Flora Lake

Flora Lake, the site of this study, lies in a kettle of the pitted outwash of Vilas County, Wisconsin. The outwash is composed of nearly horizontally bedded sand with scattered pebbles and boulders, and the underlying bedrock is of a crystalline nature (Thwaites 1929). Maximum depth of the lake is about 9 meters, and the irregular surface covers an area of 41.3 hectares.

The brown stain of the water is typical of many lakes in the vicinity, and it is thought to result from the accumulation of humic colloids. Consequently, most of the light is absorbed in the upper two meters, and mid-summer limnological observations show virtual absence of light and oxygen below six meters. Water temperatures are relatively high throughout, but a distinct thermocline is evident. As would be expected in lakes of this type, there is little carbonate (under 10 ppm) and the pH is below 6.0.

Among the more common larger aquatic plants are *Nymphaea odorata, Nuphar advena, Brasenia Schreberi, Dulichium arundinaceum, Utricularia* sp., *Ceratophyllum demersum,* and several species of *Potamogeton*. *Isoetes Braunii* is plentiful, as is the moss *Fontinalis*. The plankton of some lakes in this region has been discussed by Johnson (1954).

One hybrid and seven species of fish were netted consistently, namely, largemouth bass, bluegill, pumpkinseed, bluegill × pumpkinseed hybrid, rock bass, yellow perch, white sucker (*Catostomus commersonnii*), and golden shiner (*Notemigonus crysoleucas*). Burbot (*Lota lota*), yellow pikeperch (*Stizostedion vitreum*), and northern black bullhead (*Ameiurus melas*) were taken rarely.

METHODS

Population estimates

At the beginning of every summer during the period 1953-1956, the populations of important species of fish were estimated by mark and recapture methods (Table I). Estimations were made according to Petersen (1896) in most instances; however, the Schnabel method (Schnabel 1938) was applied to largemouth bass and my own regression modification of Petersen's method (Parker 1955) was utilized for a population composed of bluegills, pumpkinseeds, and hybrids of these two. Grouping of species in a single estimate has been shown to be inadvisible (Ricker 1948), but rapid handling made separate treatment impractical. It is questionable whether the few pumpkinseeds and hybrids in the three-fold combination

TABLE I. Summary of the numbers (Petersen estimates) of fishes present in Flora Lake, Wisconsin, during the period 1952-1956, with approximate 95 percent confidence intervals

Date	Species					
	Large-mouth bass 130-300 mm.	Bluegill Pumpkin-seed Hybrid >70 mm.	Rock bass >70 mm.	Yellow perch >80 mm.	White sucker >140 mm.	Golden shiner >55 mm.
7 -7-52	127*	33,293	1,216	10,878	1,581	1,744
	82					
	280					
7- 6-53	108*	28,238†	1,085	10,747	1,359	1,744
	70	23,459	749	7,929	1,063	733
	237	34,778	1,969	19,671	1,881	.....
6-25-54	202*	12,838†	1,517	16,916	1,570	6,508
	166	10,518	1,176	14,339	1,120	3,848
	256	16,137	2,135	20,623	2,626	21,079
7- 1-55	261*	3,898†	2,212	12,822*	1,885	11,616
	229	3,156	1,510	8,055	1,595	3,924
	303	4,991	4,132	31,413	2,305	.....
6-11-56	425	21,621	400	10,207	976	990
	348	18,952	191	5,713	716	341
	548	25,167	......	47,845	1,533	......

*Schnabel estimate. †Regression estimate.

would greatly influence the overall estimate in this case. Estimates by least-squares analysis were not used for the remaining species, since there were few recaptures and a high degree of variability in the required ratio of marked returns to the total number sampled. It is my opinion that the standard method employed yielded results that were slightly high.

The total weight of the catchable population of each species in Flora Lake at the time of estimation was based on the numerical estimates and on the average weight of fish removed during the week immediately following the marking period (Table II).

TABLE II. Average weight in grams (sample size) for each species of fish removed from Flora Lake, Wisconsin, during the week following the period of marking in 1952-1956

Year	SPECIES				
	Bluegill Pumpkinseed Hybrid	Rock bass	Yellow perch	White sucker	Golden shiner
1952*	....	86.6 (131)	19.7 (131)	209.2 (222)	....
1953	44.6 (3,568)	97.4 (41)	15.6 (389)	390.1 (98)	45.4 (13)
1954	36.0 (3,529)	93.9 (133)	23.0 (1,015)	374.8 (78)	15.5 (152)
1955	28.2 (1,070)	61.8 (72)	19.0 (222)	158.6 (71)	39.2 (118)
1956	12.4 (3,027)	48.2 (48)	16.4 (177)	308.5 (122)	36.3 (15)

*July and August.

No population estimates were made in 1952 except for largemouth bass. Under the assumption that the lake was in or near a state of equilibrium as far as the fish population was concerned, the total number present was approximated by adding the number removed in 1952 to the estimated number in 1953.

Removal

Fyke nets of ⅜-inch (0.95 cm) and 1-inch (2.54 cm) bar mesh were employed almost exclusively to remove bluegills, pumpkinseeds, hybrids, rock bass, yellow perch, white suckers, and golden shiners, while largemouth bass taken were returned to the water. A few large perch traps of wire mesh were used with little success in 1953, and in 1954 a large bay was blocked off with a seine and poisoned with rotenone. Total numbers and pounds removed are summarized in Table III.

Before removal operations began each summer, the percentage of the weight of all species present which was subsequently taken from the lake ranged from 10.2 in 1956 to 52.5 in 1953 (Table IV). The 1956 total quantity of fish removed obviously had no influence on the rates of growth measured here, since it was merely those fish which were removed in making the necessary final population estimates. The percentage removed may have been considerably more in 1955, when an unreliable estimate of golden shiners was very high and indicated that they made up over 35 percent of the grand total.

TABLE III. Numbers and kilograms of each species of fish removed from Flora Lake, Wisconsin, during the summers of 1952-1956 with effort in fyke net days as indicated

Species	YEAR						
		1952	1953	1954		1955	1956
	No. of fyke net days	123	286	405	Poison*	490	41
Bluegill Pumpkinseed Hybrid........	No.	5,055	16,943	13,276	879	6,159	3,027
	Wt.	228.0	720.6	421.0	27.9	109.9	37.7
Rock bass	No.	131	310	694	44	376	48
	Wt.	11.3	27.4	47.3	3.0	20.4	2.3
Yellow perch	No.	131	1,956	7,094	1,297	1,292	177
	Wt.	2.6	48.7	131.0	23.9	21.6	2.9
White sucker	No.	222	734	708	182	929	122
	Wt.	46.4	321.2	142.4	36.7	229.7	37.6
Golden shiner	No.	0	317	1,627	360	487	15
	Wt.	0.0	7.7	29.5	6.5	18.2	0.5

*Estimates were made before poisoning of a large bay which was blocked off with a seine.

TABLE IV. Percentage of the estimated total weight in kilograms of each species of pan and rough fish present in Flora Lake, Wisconsin, at the time of population estimation which subsequently was removed during the summers of 1952-1956

Year		SPECIES					
		Bluegill Pumpkinseed Hybrid	Rock bass	Yellow perch	White sucker	Golden shiner	All species
1952...	Est. total	1,484.9	105.3	214.3	330.7	79.1	2,214.3
	% removed	15.4	10.7	1.2	14.0	0.0	13.0
1953	Est. total	1,259.4	105.7	167.7	530.1	79.1	2,142.0
	% removed	57.2	25.9	29.0	60.6	9.7	52.5
1954	Est. total	462.2	142.4	389.1	588.4	100.9	1.683,0
	% removed	97.1	35.3	39.8	30.4	35.7	51.6
1955	Est. total	109.9	136.7	243.6	299.0	455.3	1,244.5
	% removed	100.0	14.9	8.9	76.8	4.0	32.1
1956	Est. total	268.1	19.3	167.4	301.1	35.9	791.8
	% removed	14.1	11.9	1.7	12.5	1.4	10.2

Scale and weight analyses

Scale samples were collected periodically during the five years of the study to determine whether an increased rate of growth would be in evidence on them. These were removed from the left side of the fish on a line from the front of the dorsal fin to the base of the pectoral fin. The scales were easily read dry because of their usually small size and flexible nature. Mounting between two glasses slides and projecting with a "Bioscope" at a magnification of 50 diameters proved to be satisfactory. Focus, annuli, and edge were marked on a strip of paper, from which calculations of total length at each annulus were made from nomographs similar to those described by Carlander and Smith (1944) and Hile (1950). A linear relationship between anterior scale radius and total length of the fish was found to give a sufficiently accurate prediction of length at the time of scale formation for all species (Table V). A curvilinear regression might have given a slightly higher correlation, but the small increase in the degree of accuracy does not seem to warrant the additional labor in calculation. Least-squares approximations have been used for consistency with the work of other writers; however, the methods of Wald (1940) and Bartlett (1949) which fit straight lines when both variables are subject to error might yield more realistic results.

TABLE V. Linear regressions of total length (mm) on anterior scale radius (mm x 50) for one hybrid and seven species of fish taken from Flora Lake, Wisconsin, during the period 1952-1956

Species	n	Intercept	Slope	Correlation coefficient	Error sum of squares
Largemouth bass....	479	22.8	1.4496	0.974	193,389
Bluegill............	1,119	32.6	0.9799	0.939	115,068
Pumpkinseed.......	119	30.4	0.7750	0.853	12,875
B x P hybrid.......	276	31.4	0.7908	0.891	43,552
Rock bass..........	255	35.5	0.7495	0.946	50,503
Yellow perch.......	342	47.8	1.4112	0.920	54,251
White sucker.......	285	70.2	1.3830	0.976	55,432
Golden shiner.......	184	63.7	1.1459	0.826	47,188

In order to decide whether there had been an increase or decrease in the rate of linear growth following removal, it was necessary to find a method that would permit one to decide if a down- or upswing in growth was a "normal" fluctuation. To do this, a second-degree polynomial regression of calculated total length (L) on year (A) of life ($L = b_0 + b_1 A + b_2 A^2$) was fitted to the data on the growth which took place before 1952 (Table VI). Hile (1943) reviewed the early works of Pütter (1920), Ford (1933) and Wagler (1936, 1937) on length-age functions, and related the length of rock bass to age by an equation which assumed that the ratio of the relative growth rates in successive years was constant. It is clear that the least-squares analysis utilized here only covers the period from age one to age *n*, and does not pass through zero at age zero. An approximate 95 percent confidence interval for the mean length at a given age was set about the regression, and it was agreed to call all means of calculated total lengths at annuli formed after 1952 which fell outside of this interval an increase (or decrease) resulting from removal. Since the choice of a growth curve is arbitrary, confidence limits for other possible functions likely would differ from those used in this study; however, the areas enclosed probably would agree closely. All lengths calculated from a representative scale of each fish were used; consequently, the confidence limits are inexact when the error distributions of the lengths at successive annuli of equi-aged fish are partially dependent. In addition, we must assume that the same length-scale relationship holds for all years considered, that the rare occurrence of Lee's phenomenon does not reduce appreciably the precision of the computations, and that no "abnormal" fluctuation in growth rate would have occurred had no thinning been done. For these reasons, one should attach little significance to small changes in the rate of growth as identified with the above procedure.

TABLE VI. Second-degree polynomial regressions of calculated total length (mm) at each annulus formed in or before 1952 on year of life for fishes collected from Flora Lake, Wisconsin, in 1952-1956

Species	n	b_0 (intercept)	b_1	b_2	Error sum of squares
Largemouth bass....	556	39.2	73.98	−3.542	275,895
Bluegill............	3,403	31.7	21.47	−0.639	146,997
Pumpkinseed.......	309	25.2	28.88	−0.783	23,676
B x P hybrid.......	585	27.5	25.64	−0.570	75,345
Rock bass..........	729	32.7	22.18	−0.205	76,615
Yellow perch.......	455	61.5	21.64	0.755	37,407
White sucker.......	265	64.4	86.98	−3.573	183,424
Golden shiner.......	48	54.7	35.82	−0.237	18,826

In Flora Lake, annuli were formed in all years during the period from mid-May to mid-June, with older fish being the last to lay down an annulus. Aging was not difficult, but largemouth bass and yellow perch had occasional check marks and/or false annuli.

The other possible change in rate of growth following thinning is that in the weight of an individual at a given length. Schuck (1942) has used the covariance technique to analyze the difference between the fatness of tagged and untagged trout. Similar methods have been employed here on equal sized, randomly selected samples of fish collected in 1952 and in 1956. Logarithmic values were used to give nearly linear relationships between weight and length which could be subjected to extensive analysis. Adjusted means were compared, i.e., the mean weight in 1952 and in 1956 computed at the mean of the lengths of both years combined. If the slopes of the two regressions differed significantly, the error sum of squares used in testing for a difference between adjusted means was computed in the manner of Mood (1950). It should be pointed out that the covariance technique as applied to weight-length data gives only approximate results, since neither variable can be measured without error.

RESULTS

Largemouth bass

Growth

Previous to the initiation of removal operations in 1952, the linear growth rate of largemouth bass in Flora Lake was similar to that of bass in other lakes of northern Wisconsin as given by Bennett (1937). A comparison of the average calculated total lengths in millimeters at each annulus is made below.

Age	*Northern Wisconsin*	*Flora Lake*
1	71	108
2	165	174
3	246	232
4	297	284
5	335	315
6	353	345
7	386	379
8	424	403
9	450	437
10	470	470

It appears that the Flora Lake bass grew faster during the first two years of life, but this may be due to the fact that Bennett assumed direct proportionality of growth to scale radius with a zero intercept, whereas an intercept of 22.6 millimeters has been used here. It is likely that the bass in Flora Lake grew at a rate throughout life which was slightly behind the northern Wisconsin average.

TABLE VII. Calculated total length (mm) of Flora Lake fishes at the time each annulus was formed in or before 1952 as estimated from the equations given in Table VI, with approximate confidence intervals

Species	Age	n	Actual mean	Estimated mean	95% confidence interval
Largemouth bass	1	139	107.5	109.7	98.2-121.2
	2	130	174.2	173.0	166.1-179.9
	3	113	231.5	229.2	227.0-231.4
	4	72	283.5	278.4	272.9-283.9
	5	45	315.0	320.5	308.0-333.0
	6	28	345.1	355.5	335.1-375.9
	7	13	379.1	383.4	354.1-412.7
	8	10	402.6	404.3	365.4-443.2
	9	5	437.0	418.1	368.7-467.5
	10	1	470.0	424.8	364.0-485.6
Bluegill	1	876	52.9	52.6	51.2- 54.0
	2	836	72.2	72.0	71.2- 72.8
	3	772	88.2	90.3	89.9- 90.7
	4	387	110.0	107.4	106.5-108.3
	5	289	123.9	123.0	121.0-125.0
	6	131	137.6	137.5	134.4-140.6
	7	73	148.8	150.6	146.2-155.0
	8	32	163.1	162.5	156.7-168.3
	9	5	165.4	173.1	165.8-180.4
	10	2	175.5	182.5	173.5-191.5
Pumpkinseed	1	84	53.6	53.3	43.7- 62.9
	2	84	79.2	79.9	75.7- 84.1
	3	70	105.7	104.8	102.0-107.6
	4	50	127.6	128.2	117.5-138.9
	5	20	150.6	150.0	130.1-169.9
	6	1	171.0	170.3	140.0-200.6
Bluegill x Pumpkinseed hybrid	1	152	53.1	52.5	44.7- 60.3
	2	146	75.7	76.5	72.7- 80.3
	3	140	98.8	99.3	97.6-101.0
	4	99	121.5	121.0	113.4-128.6
	5	39	143.8	141.5	126.9-156.1
	6	7	153.9	160.9	138.4-183.4
	7	2	173.0	179.1	147.7-210.5
Rock bass	1	160	56.4	54.7	49.9- 59.5
	2	157	75.0	76.3	73.2- 79.4
	3	147	95.3	97.4	96.3- 98.5
	4	109	118.4	118.1	115.8-120.4
	5	83	139.0	138.5	134.0-143.0
	6	32	164.6	158.4	150.9-165.9
	7	21	182.2	177.8	166.9-188.7
	8	11	194.3	197.0	182.4-211.6
	9	6	208.3	215.7	197.0-234.4
	10	3	220.7	234.0	210.9-257.1
Yellow perch	1	212	83.5	83.9	79.8- 88.0
	2	154	109.4	107.8	106.9-108.7
	3	59	131.2	133.2	127.6-138.8
	4	19	158.9	160.2	148.3-172.1
	5	8	188.5	188.6	169.4-207.8
	6	2	229.0	218.5	191.0-246.0
	7	1	249.0	250.0	213.2-286.8
White sucker	1	130	147.9	147.8	128.0-167.6
	2	78	224.6	224.1	220.3-227.9
	3	40	289.6	293.1	264.0-322.2
	4	12	366.0	355.1	293.6-416.6
	5	5	402.0	410.0	310.6-509.4
Golden shiner	1	22	89.6	90.3	34.5-146.1
	2	18	126.9	125.4	106.6-144.2
	3	8	158.5	160.0	47.2-272.8

Table VII gives the mean calculated length at each age before removal as determined from the actual totals and as estimated from the quadratic equation in Table VI. The quantities estimated agree well with the actual ones (Fig. 1), thus confirming the validity of the estimation method. Large differences are found only at ages 9 and 10, where few fish were represented. Using the appropriate intervals from Table VII, the growth of the bass after 1952 was examined with the hope of finding a marked increase. Changes were decided on as agreed earlier, and (+), (—), or (0) were used to identify them (Table VIII). In 1953, the year after the first reduction, only four- and five-year old bass showed an increase. These two year classes maintained the increase during succeeding years. The 1950 year class exhibited a negative change, while increases were shown by the 1951 year class. The following year class was below expectation in 1955, but had gained

TABLE VIII. Calculated total lengths (mm) at annuli formed in successive years after 1952 by each year class of fishes taken from Flora Lake, Wisconsin, in 1953-1956 with sexes combined; significant changes in growth rate indicated by + or − and no change by °

Year	YEAR CLASS												
	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955
Largemouth bass													
1953						335^{+} 5*	317^{+} 3	224^{-} 3	171° 9	102° 47			
1954						405^{+} 1	352^{+} 3	258^{-} 2	233^{+} 6	178° 25	103° 207		
1955							382^{+} 1	281^{-} 1	282° 5	217^{-} 18	172° 130	77^{-} 189	
1956									345^{+} 1	291^{+} 1	221^{-} 26	170° 14	104° 14
Bluegill													
1953	168^{-} 1	168° 7	160° 12	151° 29	135° 100	123° 61	99^{-} 370	91^{+} 63	77^{+} 39	51^{-} 73			
1954		182° 3	170° 1	159° 7	153° 52	140° 23	120^{-} 239	104^{-} 12	88^{-} 20	72° 67	47^{-} 174		
1955					158° 3	151° 7	137° 50	124° 8	112^{+} 12	96^{+} 52	72° 174	48^{-} 309	
1956						170^{+} 1	163^{+} 1	160^{+} 1		137^{+} 1	107^{+} 72	80^{+} 235	50^{-} 20
Pumpkinseed													
1953						129^{-} 1	108^{-} 2	94^{-} 14	53° 1				
1954						136° 1	121^{-} 2	110^{-} 11	77° 1	54° 19			
1955								126^{-} 1	101^{-} 1	90^{+} 19	53° 1		
1956									138° 1	129^{+} 15	95^{+} 1		
Bluegill x Pumpkinseed hybrid													
1953				156° 3	144° 8	135° 27	107^{-} 31	83^{-} 6	80° 6	49° 26			
1954					161° 6	154° 16	126^{-} 22	100^{-} 5	102^{+} 5	73° 26	53° 112		
1955						151° 1	144° 4		125° 4	97^{-} 18	84^{+} 87	49° 82	
1956							156° 3			122° 10	124^{+} 19	82^{+} 64	57° 4
Rock bass													
1953		189^{-} 1	212^{+} 2	204^{+} 2	157° 21	139° 16	107^{-} 33	91^{-} 10	72^{-} 3	56° 52			
1954		210^{-} 1	234° 2	222^{+} 1	178° 11	172^{+} 12	150^{+} 28	125^{+} 8	99^{+} 3	79° 52	56° 62		
1955					172^{-} 1	189^{+} 2	167^{+} 4	156^{+} 5	114^{-} 1	109^{+} 20	81^{+} 50	52° 32	
1956						209° 1	193^{+} 3	171^{+} 2	140° 1	146^{+} 4	119^{+} 23	76° 17	52° 1
Yellow perch													
1953				243° 1	208° 5	179° 7	151° 24	131° 62	109^{+} 51	84° 61			
1954					228° 4	201° 5	178° 7	148^{-} 19	125^{-} 23	109^{+} 51	84^{-} 151		
1955							174^{-} 2	166 2	151° 2	124^{-} 23	101^{-} 128	77^{-} 11	

TABLE VIII (Continued)

Year	Year Class 1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955
1956									173° 2	142^{-} 9	122 70	108° 11	83° 21
White sucker 1953						435° 1	378° 3	330^{+} 10	244^{+} 42	178^{+} 23			
1954							426° 2	439^{+} 1	324^{+} 3	286^{+} 16	148° 87		
1955									364° 1	357^{+} 4	238^{+} 54	162° 120	
1956										455^{+} 1	340^{+} 12	274^{+} 67	194^{+} 20
Golden shiner 1953								155° 10	130° 4	94° 67			
1954									152° 4	124° 49	88° 106		
1955										142° 32	118° 66	88° 3	
1956											152° 10		

*Number of fish.

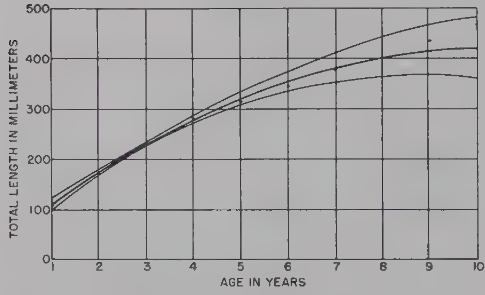

FIG. 1. Pre-treatment theoretical growth curve for largemouth bass from Flora Lake, Wisconsin, with the actual means and an approximate 95 percent confidence region shown.

enough to overcome the deficit by 1956. During the first year of life, every year class was within the normal range except that of 1954, which fell far below. This is probably the result of a very successful year class which caused stunting within that age group. In considering the bass as a whole, one must conclude that there has been no significant change in the linear rate of growth (Fig. 2).

Lee's phenomenon, an apparent decrease in the calculated lengths as determined from successively older groups of fish, could be demonstrated only for the 1953 and 1954 year classes. Averages for the yearlings of the 1953 year class were computed as 108, 103, and 91 millimeters, based on 77, 104, and 26 fish collected in 1954, 1955, and 1956, respectively. The yearlings of the 1954

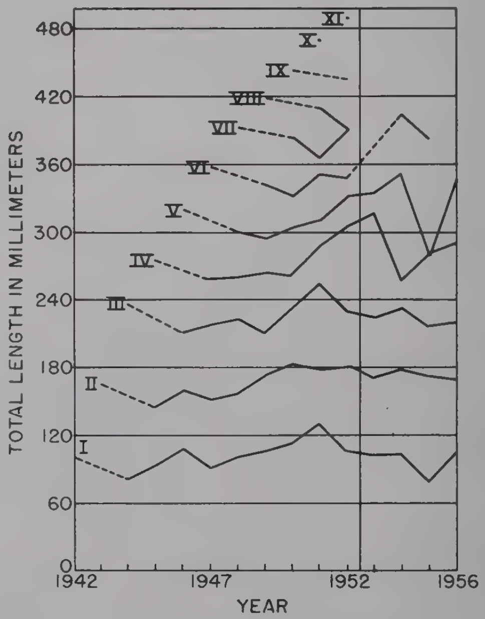

FIG. 2. Fluctuations in the mean, calculated total length of Flora Lake largemouth bass in each age group.

year class averaged 81 and 74 millimeters according to 72 and 117 scale samples examined in 1955 and 1956, respectively.

A somewhat better picture is obtained when the plumpness of bass taken in 1952 is compared with that of those taken in 1956 (Table IX). Although there was a significantly smaller slope of the logarithmic regression of weight on length in 1956 when compared with that in 1952, the adjusted mean weight in 1956 was higher than it was in 1952.

Table IX. Weight-length relationships (natural logarithms) for fishes collected from Flora Lake in 1952 and 1956, with significant and highly significant differences between years indicated by * and **, respectively

Species	Year	n	Intercept	Slope (1)	Adjusted mean (2)	Difference between years (1)	(2)
Largemouth bass..	1952	119	−12.60039	3.22203	5.00665	**	**
	1956	119	−11.76539	3.08432	5.08912		
Bluegill..........	1952	191	−10.95669	2.98833	3.22555	**	**
	1956	191	−12.06153	3.18268	3.04166		
Pumpkinseed.....	1952	17	−11.49236	3.12343	3.89496	**	*
	1956	17	−25.05247	5.90165	4.02139		
B x P hybrid.....	1952	71	−11.76449	3.17696	3.46265	*	
	1956	71	−12.91231	3.41708	3.46572		
Rock bass........	1952	52	−11.24900	3.05464	3.81370	**	
	1956	52	− 8.50133	2.49797	3.81638		
Yellow perch......	1952	62	−12.28443	3.12003	2.77284	**	**
	1956	62	−10.62066	2.75912	2.69485		
White sucker.....	1952	73	−11.01743	2.91365	5.55440	*	**
	1956	73	−11.63834	3.04022	5.65338		
Golden shiner.....	1952	8	− 4.04647	1.56823	3.98394	*	**
	1956	8	−13.34188	3.34451	3.78428		

Yield

Creel records were difficult to obtain on the voluntary basis employed, but examination of the completed cards and a record book of Dairymen's Country Club, on whose property Flora Lake is located, gave reasonably accurate returns except for the first part of 1952. There has been a definite increase in the yield of largemouth bass to fisherman (Table X), and this is correlated negatively with the size of the bluegill population (Table I). The same situation has been encountered in Ridge Lake, Illinois, by Bennett (1954). Although data on angling effort were lacking, the presence of the same number of boats kept at the landing (3) and my daily observations convinced me that the effort was nearly constant.

Table X. Changes in the estimated total weight in kilograms of largemouth bass in Flora Lake, Wisconsin, during 1952-1956

Year	130-300 mm.	Over 300 mm.	Total	Net change	Removed by anglers after estimate
1952	22.6	151.3	173.9		15.4(?)
1953	10.3	68.9	79.2	− 79.3	19.6
1954	13.9	93.0	106.9	+ 47.3	42.3
1955	29.7	198.8	228.5	+163.9	65.9
1956	36.7	245.6	282.3	+119.7	

Changes in total population

Bennett, in his Ridge Lake study, found no apparent relationship between the number of spawning adults and the number of bass fry produced. In an earlier work (1945), he mentions that a heavily overfished population of bass was able to reproduce enough young to replace those individuals caught. He also points out that the number of bass fry observed in Ridge Lake is related negatively with the number of bluegills present in the lake, and in some years all of the bass fry were eliminated by the bluegills. The latter condition has been shown to exist in some southern ponds (Swingle and Smith 1943).

In Flora Lake there has been a decided yearly rise in the number of bass between 130 and 300 millimeters in length since 1952 (Table I). The estimated total weight in this group at the time of population estimation in 1952 to 1956 was 22.6, 10.3, 13.9, 29.7, and 36.7 kilograms, respectively. After 1952, it was almost impossible to catch largemouth bass over 300 millimeters with fyke nets. For this reason and also because bass under 130 millimeters were subject to a possibly higher mortality after marking, the number and weight of fish within these limits was used as an index to the magnitude of the total population.

During the first summer of the experiment (1952), an estimation of bass over 300 millimeters was made. An analysis indicated a population of 235 fish which weighed 151.3 kilograms or 87.0 percent of the total weight of bass over 130 millimeters. If this same relationship was maintained through 1956, the total weight would have risen to 282.3 kilograms or 6.8 kilograms per hectare (Table X). In 1952 and 1956, the bass constituted 7.3 percent and 26.3 percent, respectively, of the total weight of all species; however, this striking increase is partially the result of a reduction in the total weight of all species per hectare from 57.6 kilograms in 1952 to 26.0 kilograms in 1956.

The net change in the total weight of bass is a measure of the increase or decrease in the standing crop after losses from angling and natural mortality have taken place. The greatest change occurred between 1954 and 1955, namely a 163.9-kilogram addition (Table X). Presumably, the removal efforts had their most pronounced effect on the growth of the population during the growing season of 1954, two years after their initiation. Up until 1954, 34.2 kilograms per hectare had been removed, and in 1954, 20.9 kilograms per hectare were removed.

Bluegills, pumpkinseeds, and bluegill × pumpkinseed hybrids

The growth of bluegills prior to the onset of netting in 1952 was very slow, with annual increments being less than 25 millimeters. Some indication of their stunted condition can be had by comparing their average length at a given age, say five, with the corresponding length of bluegills in other areas. Kuehn (1949) gives an average of 180 millimeters for fish from Minnesota lakes, whereas those from Flora Lake where only 124 millimeters. Specimens from Third Sister Lake, Michigan, averaged 188 millimeters (Brown and Ball 1943) while bluegills taken from Onized Lake, Illilnois, 500 miles to the south, already had reached 188 millimeters at age four (Bennett 1945).

Agreement between actual and estimated, mean, calculated lengths is excellent; that is, the polynomial provides a good fit to the length-age data (Table VII). Examination of the calculated total lengths after 1952 shows that a definite increase was not apparent until 1956, when all year classes except 1955 were higher than if a normal fluctuation had occurred (Table VIII). Even though members of the 1954 year class were below expectation as yearlings, they reached a greater length as two-year olds than any like-aged group in the past. The increase in the two- and the three-year olds was of high significance, since these fish made up 75.4 and 23.3 percent, respectively, of the total catchable population of bluegills in 1956.

Bluegills are dominant among the three sunfishes considered here. Samples netted in 1953 and 1956 yielded the following composition expressed as percentages:

	Bluegill	*Pumpkinseed*	*Hybrid*
1953	88.5	4.5	7.0
1956	86.0	0.6	13.4

The increase in the population of bluegills between 1955 and 1956 (Table I) was the result of the recruitment of a large 1954 year class which previously had been unavailable to the nets. It would seem that the lower density of the population had enabled a higher percentage of the bluegill-hatch to survive. Swingle and Smith (1943) claim that bluegills, when overpopulated, will eat many or all of their own eggs. The thinning process in Flora Lake apparently had reduced the numbers to a point where cannibalism was of no consequence, and a dominant year class erupted.

Although the bluegills captured in 1956 had shown an increase in rate of linear growth, they were considerably thinner at the mean length than those in the 1952 sample (Table IX). The difference between the adjusted logarithmic means may be explained in part by the fact that the average length of fish in 1956 was less than in 1952, and it is often true that large individuals are fatter than small ones (Beckman 1948).

Analysis of the sexual composition of the 1956 sample yielded a ratio of 104 males for every 100 females, with females predominating above age two. The growth rates of the two sexes belonging to recent year classes were nearly identical.

Lee's phenomenon could not be identified positively in any of the year classes of bluegills, pumpkinseeds, or hybrids, except possibly in the 1949 year class of bluegills.

Pumpkinseeds grew at a higher rate before 1952 than did the bluegills or hybrids. Carbine and Applegate (1948) described a similar occurrence in Deep Lake, Michigan, from which the entire population was removed by poisoning. In their study, bluegills were found to grow faster than the other two, in contrast with the situation here. Hubbs and Hubbs (1931, 1933) have observed that some hybrid centrarchids outgrow both of the parent species in tanks under laboratory conditions.

In Flora Lake, pumpkinseeds belonging to the 1953 year class increased significantly in linear rate of growth during their second and third years of life. Usually, however, there was a decrease in the growth of the older fish netted before 1956 and little or no change in the younger fish (Table VIII). Pumpkinseeds in 1956 had a distinct advantage in adjusted mean weight when compared with the 1952 specimens (Table IX). Although no difference between the rates of linear growth by sex could be detected, females were slightly heavier than males at a given length.

Attention should be called to the marked reduction in the percentages listed above of pumpkinseeds taken in 1956 as compared to 1953. During 1956, only 17 pumpkinseeds were among the 3027 members of the bluegill-sunfish-hybrid combination removed. Of these, one was two years old, 15 were three years old, and one was four years old. Could this small population have become predaceous on the numerous young of their near relatives, thereby moving from a normal last to first place in growth among the three?

The theoretical pre-treatment growth curve of the bluegill × pumpkinseed hybrids was midway between those of the parents. Important gains in the rate of linear growth were registered by the 1951 year class in 1954, by the 1953 year class in 1955 and in 1956, and by the 1954 year class in 1956 (Table VIII). In contrast with the parent species, hybrid females of recent year classes (1952, 1953, 1954) grew slightly faster linearly than did the males.

The adjusted mean of the logarithmic weights in 1952 did not differ significantly from that in 1956; however, the slope of the 1956 regression was much higher than the slope in 1952 (Table IX).

It should be emphasized that significant increases in the rate of linear growth occurred in the 1953 and 1954 year classes of bluegills, pumpkinseeds, and hybrids, thereby indicating that the three react similarly to the stimulus provided by the thinning operation.

Rock bass

The earliest recorded study on the growth of rock bass in lakes of the immediate vicinity (Trout and Muskellunge) was that of Wright (1929). He used direct proportionality between body and scale lengths and as a result, his growth records are not directly comparable with those of rock bass in Flora Lake. Hile (1941, 1942) analyzed the growth rates of rock bass in Silver, Allequash, and Nebish Lakes, in addition to the two lakes mentioned above. His attempts to relate fluctuations in growth to air temperature and amount of precipitation met with some success. Although his data are presented in terms of calculated standard length at each annulus, the rate of growth was quite similar to that of Flora Lake rock bass.

It has been known for some time that rock bass respond favorably to a severe reduction in population density (Beckman 1941, 1943). Significant deviations from the estimated pre-treatment means appeared in over half of the year classes by 1954. In 1956, three-year-old fish were 20 millimeters longer than the upper limit of the normal expected value, and four-year-old fish averaged 25 millimeters above the upper bound (Table VIII). Even though the fish showed an increase in linear rate of growth, a comparison of the adjusted mean weights yielded no real differences between individuals collected in 1952 and individuals collected in 1956 (Table IX).

The relatively few rock bass in Flora Lake are highly piscivorous, and apparently do not associate with other species except to feed on them. Why these fish respond so quickly and positively in their rate of growth to a lower total population density is a question which bears need of future investigation. In addition, analysis of the growth response is complicated by the fact that there was a general increase in the numbers of rock bass from 1952 through 1955 (Table I).

Sample sizes were usually insufficient to demonstrate the occurrence of Lee's phenomenon, although some evidence was found among members of the 1947 year class. As was the case with all species, no pre-treatment sex-composition data were obtained by Johnson, *et al.;* consequently, comparisons of sex ratios could not be made. In 1956, little difference was noted between the growth rates of sexes during the first three years of life; however, Hile's studies established that males grow distinctly better than females in later years.

Yellow perch

The perch in Flora Lake ranked second in numbers during most of the period 1952-1956 (Table I), and they grew much more slowly than did perch in neighboring Nebish, Weber, and Silver Lakes (Schneberger *op. cit.*) and in Curtis Lake (Churchill *op. cit.*). Their computed growth curve was the only one having a positive coefficient for the squared term of the polynomial (Table VI), that is, the curve was concave upwards. This may indicate that the few larger perch reached a length where they were able to prey upon their numerous kin, thereby increasing their rate of growth. Estimated means are very near to the actual values except for age six where there is a discrepancy of 10.5 millimeters (Table VII). After examining the mean calculated lengths for growth following 1952 (Table VIII), one necessarily concludes that there has been no increase in the rate of growth, but rather a decrease. More than likely, this is due to the presence of large, recent year classes, while the total perch population has remained relatively stable (Table I). Furthermore, individuals were thinner in 1956 than they were in 1952 (Table IX).

Schneberger (*op. cit.*) concluded that male and female perch grow at approximately the same rate. The same conclusion has been reached for Flora Lake perch, at least for the younger individuals.

Males were scarce among the older age groups, as was noted also by Eschmeyer (1937).

White suckers

The pre-treatment growth rate of the white suckers in Flora Lake was considerably better than the growth rate of suckers in nearby Muskellunge Lake (Spoor 1939), with Flora Lake fish attaining a length of 148 millimeters in one year. After 1952, the suckers, which ranked second in total weight (Table IV), began to grow more rapidly (Table VIII). This increase is of considerable interest, since the fish were not stunted before the start of removal operations, but still had an inherent ability to grow faster. In addition, as with the rock bass, there was an increase in numbers to a peak in 1955 (Table I). In contrast with the rock bass, however, the suckers taken in 1956 were fatter than individuals netted in 1952 (Table IX).

The separation of calculated lengths according to sex failed to show a real difference between males and females, at least through age three.

Golden shiners

The relatively small numbers of golden shiners available for the computation of a theoretical pre-1952 growth curve caused very wide confidence intervals (Table VII). As a consequence, no significant change in the rate of linear growth could be detected (Table VIII); however, fish sampled in 1956 were lighter (adjusted mean) than those taken in 1952 (Table IX).

Although the population estimates gave large numbers for golden shiners (Table I), their low frequency of capture in fyke nets lends support to the belief that the high estimates were the result of a much greater mortality among the marked individuals, possibly resulting from handling. It is questionable whether more than 2000 catchable golden shiners have been present in Flora Lake at any time during the past five years.

SIGNIFICANCE

The rather inconsistent responses in growth, presumably resulting from a reduction in the density of the population, are rather remarkable. For example, although the rock bass and the yellow perch were thinned similarly (Table IV), the growth rate of the former changed favorably while that of the latter decreased. The largemouth bass, on the other hand, apparently did not benefit from the removal operations except for a slight increase in adjusted mean weight.

At the present time, I do not know of any thorough thinning studies which have shown definitely that the growth rate of the largemouth bass is density-dependent, but one intuitively feels that it must be. In July 1954, largemouth bass from Dadek Lake, Wisconsin, which were stunted when compared with those from Flora Lake, were transferred to Corrine Lake, Wisconsin. The latter body of water had a bass-density of less than one-fourth of that in Dadek Lake. A preliminary analysis of data collected in September 1954 and June 1956 showed that an initial spurt in growth occurred among one- and two-year old fish during the same summer as the stocking; however, this rate of growth soon subsided. As a result, the bass were no longer in 1956 than would have been expected had they remained in Dadek Lake. Before one is able to draw a valid conclusion here, it is necessary to investigate the effect of reducing the bass population itself. Perhaps some information could be obtained by continuing the elimination of bass from Dadek Lake, with an eye toward evaluating the growth of the remaining bass. In spite of the fact that the bass in Dadek and Flora Lakes have different rates of growth, a common ancestry may have the consequence that neither will grow faster under conditions of reduced density, and the introduction of marked bass from both lakes into another might shed some light on this problem.

As mentioned previously, perch in Sweden and in England (Windermere) reacted differently after a decrease in numbers; however, these contrasting results are not directly comparable because Alm (*op. cit.*) moved individuals to other waters while LeCren (*op. cit.*) described a perch population which was reduced *in situ*. Subsequent to severe winterkill, the growth of perch in Duck Lake and Green Lake, Michigan, rose to 61 and 35 percent, respectively, above the normal mean (Beckman 1950). This suggests that the perch in Flora Lake might have grown faster if more of them had been removed, that is, more than 39.8 percent of the standing crop (Table IV).

As for the rock bass, these studies confirm those of other workers in that this species is nearly always the first to grow faster following a reduction in density. This result, coupled with the erratic changes exhibited by the other species, leads one to speculate on some possible explanations. The answer may lie in the genic control of the hormonal complex which governs most of the bodily processes. Future studies of the type executed here might be pointed toward an evaluation of the physiological mechanisms correlated with changing rates of growth.

From the statistics on removal (Table IV), it appears that the differential rates of removal play but a small role in determining what the response of a particular species will be. There is some likelihood that a careful examination of the behavior traits of different species will reveal an influence on the rate of growth after some of the other fish have been destroyed.

Larkin (1956) reviewed briefly the voluminous literature concerning the intricacies of competition between species, and made special reference to works concerning fishes. In Flora Lake, it would seem that any attempt to analyze such interrelationships which affect the growth of so many species would prove futile, particularly since other variables known to be of some importance were not measured (*e.g.,* food supply). It may be that future efforts will resolve the problem by finding a minimal density not reached in these experiments which must be attained before the growth of species unaffected here is stimulated.

SUMMARY

Flora Lake, a 41.3-hectare body of water in northern Wisconsin, was the site of a five-year program in which the density of fishes was reduced in an attempt to increase the growth rates of largemouth bass and pan fish. Fyke nets were utilized yearly in removing large numbers of a hybrid and six species, the total quantity removed ranging up to 1125.6 kilograms or 52.5 percent of the catchable standing crop at the time of population estimation in the early summer.

Scale samples, which were collected periodically, were used in the back-calculation of the total length at each annulus. A linear function was employed for every species to describe the relationship between the radius of the anterior part of the scale and the total length of the fish.

A second-degree polynomial was fitted to the data on the calculated total length at each annulus formed in or before 1952, in other words, a pretreatment growth curve was formulated as were appropriate confidence intervals for the means. It was agreed that the mean, calculated total lengths after 1952 which fell outside of the confidence intervals would be termed significant changes in the rate of growth.

The covariance technique was used to analyze the differences between the slopes of the weight-length regressions and the adjusted, mean weights of specimens collected in 1952 and in 1956.

No important changes occurred in the linear growth rate of largemouth bass; however, in 1956, individuals had a higher adjusted, mean weight than in 1952. In addition, the estimated total weight of bass over 130 millimeters in length increased from 4.3 to 6.8 kilograms per hectare, and the yield to anglers rose from 15.4 kilograms in 1952 to 65.9 kilograms in 1955, although the effort remained nearly constant.

Bluegills, pumpkinseeds, and hybrids of these two species belonging to recent year classes (1953 and 1954) responded favorably in linear rate of growth after the reduction in their numbers, but only the pumpkinseeds were heavier at the overall mean length. Presumably because of the virtual elimination of cannibalism, the 1954 year class of these sunfishes was highly successful, and the catchable population erupted from a low of 3900 in 1955 to 21,600 in 1956.

Rock bass in Flora Lake exhibited a marked increase in their linear growth rate, particularly by members of the 1949, 1950, 1952, and 1953 year classes, even though the total number of rock bass present reached a peak in 1955. A difference could not be demonstrated between the adjusted, mean weight in 1952 and in 1956.

Yellow perch were thinner and grew more slowly after the initiation of removal operations than they did before. This is attributed to (a) no real change in the total numbers of perch during the study, and (b) possible intra-year class stunting in a population composed primarily of young fish.

A relatively fast-growing population of white suckers was able to respond to the lowered overall density in a positive manner, *i.e.,* by growing faster, in spite of a continued rise in their own numbers through 1955.

The linear growth rate of golden shiners in Flora Lake did not change, but as among the perch, individuals were lighter at the mean length. Their population size was thought to be greatly overestimated due to a possibly higher mortality of marked fish.

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GAMBEL OAK IN WEST-CENTRAL COLORADO

Harry E. Brown[1]

Introduction

Growing in a belt along the hillsides of western Colorado are several million acres of brush. Gambel oak (*Quercus gambellii* Nutt.)[2] is the most common brush species, occupying about one million acres in nearly pure stands. Near its lower elevation limit at about 7,000 feet the oak is associated with pinyon pine and juniper, while at elevations approaching 9,000 feet it mingles with aspen and spruce.

Oak brush has long been a subject of controversy. Many land managers look at the brush-covered hillsides and see the importance of oak in stabilizing the soil, in retarding snowmelt, and in providing browse for deer and elk. Some of these observers are actually experimenting to find ways of increasing oak brush. Others look at these same hillsides and see oak stands too dense for their livestock to graze. They see oak brush using water and nutrients in deep, fertile soils that might otherwise be producing more forage for their cattle and sheep. They wish to kill the oak brush and replace it with grass and forbs. Further controversy exists regarding the successional position of oak brush. Some persons contend that it has spread and thickened since the early days of settlement and represents a secondary stage in succession while others consider it to be a relatively stable climax.

The study reported here is intended to help reconcile these views by providing (1) information concerning the characteristics of oak brush and its environment in west-central Colorado, and (2) evidence as to whether the extent and density of oak brush are changing now or have changed since the time of early settlement.

History

Gambel oak in west-central Colorado appears to have been abundant for several centuries on many of the sites it now occupies. Wormington (1947) provided a clue to the early existence of oak brush in his statement that acorns were a food of the "Basketmaker" Indians who lived in this area from before the time of Christ until about 700 A.D.

In describing the vegetation of the Uncompahgre Plateau during his expedition of 1776, Father Escalante reported many "small oaks" (Hafen, 1948). This same area has an abundance of Gambel oak today.

Detailed observations of vegetation types in the area were made by Sudworth (1900) during his official survey of the White River and Battlement Mesa Forest Reserves. He reported that in 1898 "Large areas are densely covered with this growth (oak brush) usually ranging from the low sage mesas, 7,000 feet, up to the aspen belt, 8,000 to 8,500 feet, patches of both oak and aspen often mingling.

"As a brush, which is the most common form, its dense thickets cover all the dry, sandy, and gravelly knolls and foothills below the forest-forming timber trees. As a tree it is confined entirely to the deep, rich soils of bench lands and gentle slopes. . .

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[1] Forester, Rocky Mountain Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, with central headquarters maintained in cooperation with Colorado State University at Fort Collins, Colorado.

[2] Nomenclature of plant species follows that of Harrington (1954). In regard to *Q. gambellii*, Harrington states: "This is a complex and variable species. However, the various segregates that have been proposed are of no value for Colorado plants."

"The brushy forms are slender and from 2 to 12 feet high. Tree forms range from 4 to 10 inches in diameter and frequently 14 to 24 inches, while the common height is 12 to 25 feet."

Sudworth further implies the long-time existence of the type by his statement "There are in the reserve low-lying brush-covered hills of vast extent, where, very probably, from the nature of conditions, forest trees have never existed and will never exist."

Throughout the years fire may have influenced the extent and density of oak brush more than any other factor. Early reports describe numerous fires throughout western Colorado between 1878 and 1905, with the greatest ones probably occurring during the first part of that period. Most fires were said to have been started by Indians who used them as a means of heading off game and providing a supply of winter firewood (Fritz, 1941). They were also used to harass the white settlers. Sudworth (1900) stated that the Indians allegedly attempted a general burning in the 1880's to drive all the large game out of the state.

Even after the Indians were removed to reservations in 1881, fires were still common for many years. Stockmen often used fire in an attempt to thin the brush so they could move livestock more easily, and burning was considered to be an effective means of increasing grass production.

Campfires were frequently neglected, and seldom was an effort made to suppress the forest or brush fires that resulted from them.

Grazing use may also have affected the extent and density of oak brush; however, no published evidence to this effect has been found. Certainly the influence of grazing on spread of brush would be difficult to establish by casual observations only.

Reports from neighboring regions contain contrasting views on the successional position of oak brush. In southern and southwestern Colorado it appears to be a secondary stage of succession. Costello points out that many oak communities in that area have developed in the wake of fires and logging which removed virgin stands of ponderosa pine and Douglas fir (Harrington, 1954).

In central Utah, on the other hand, Baker and Korstian (1931) considered the brush lands to have reached their climax type, with climate and soil precluding the invasion of conifers. Their studies revealed no dynamic successional changes in the type.

CLIMATE

The climate of the oak brush type is characterized by annual precipitation of about 15 inches, mean annual temperature of 47°F, and a growing season of about 136 days (Table I). The data were obtained from four Weather Bureau stations in or adjacent to the oak brush type (U. S. Weather Bureau, 1933, 1956). These data provide only an approximation of the oak brush climate, for all the stations are in valley bottoms rather than on hillsides where the brush grows.

TABLE I. Summary of climatic data from Weather Bureau stations in the brush type of west-central Colorado

	MEAN PRECIPITATION (Inches)				
	Collbran	Crawford	Glenwood Springs	Paonia	All Stations
January	1.16	.77	1.56	1.30	1.20
February	1.18	.51	1.40	1.28	1.09
March	1.54	.55	1.57	1.44	1.28
April	3.13	.87	1.59	1.50	1.77
May	1.37	.89	1.30	1.31	1.22
June	.79	.81	1.02	.69	.83
July	1.16	1.25	1.39	.99	1.20
August	1.49	1.20	1.69	1.31	1.42
September	1.51	1.16	1.39	1.34	1.36
October	1.42	1.11	1.26	1.45	1.31
November	1.01	.87	1.08	1.05	1.00
December	1.09	.81	1.34	1.26	1.12
Annual	16.85	10.80	16.59	14.92	14.80
Approx. years of record;	61	14	65	60	
	Mean temperature (degrees Fahrenheit)				
January	21.6	25.4	23.4	25.1	23.9
February	27.6	26.9	28.8	31.1	28.6
March	36.0	35.2	37.5	38.8	36.9
April	45.8	42.9	46.7	47.7	45.8
May	54.0	52.0	54.9	56.1	54.2
June	62.4	61.9	62.6	64.1	62.8
July	68.6	67.8	68.8	71.1	69.1
August	66.6	65.9	67.3	69.0	67.2
September	58.7	58.4	59.9	61.3	59.6
October	47.5	48.2	49.3	50.7	48.9
November	34.9	37.2	36.3	38.7	36.8
December	24.3	25.4	25.7	28.0	25.8
Annual	45.7	45.6	46.8	48.5	46.6
Approx. years of record;	50	13	47	45	
Growing season (average number of days from last killing frost to first killing frost)	126	137	120	160	136
Years of record;	29	13	26	28	

METHODS

To learn more about the characteristics of oak brush and its environment in west-central Colorado, 48 sites were studied in detail during the summers of 1953 and 1954 (Fig. 1). These sites were located in areas where relatively dense, pure

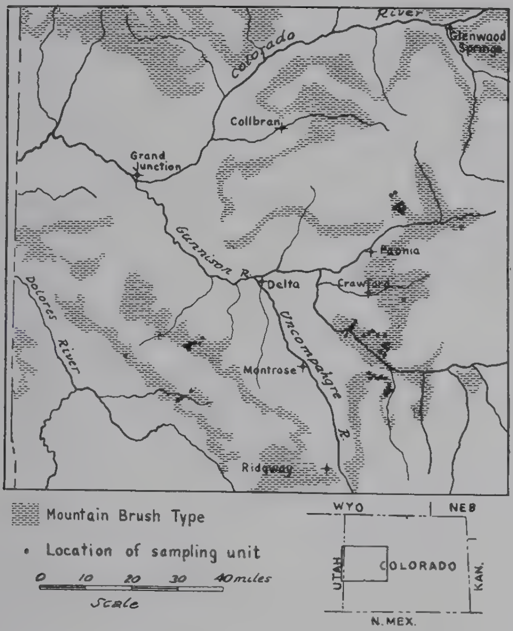

FIG. 1. Map of west-central Colorado, showing the mountain brush type and location of sampling units. Oak brush stands comprise about one third of the mountain brush type.

stands of oak are interspersed with openings. Pure oak stands were selected because they appear to present a more serious grazing problem than stands that contain a mixture of brush species. Mixed stands usually contain several browse species that are much more palatable to game and livestock than Gambel oak. Openings between oak stands were studied at the same time so that herbage production, forage utilization, and soil might be compared.

Slope, aspect, elevation, and topography of each site were recorded, as well as the geologic formation from which the soil was developed. Mancos shale, Dakota sandstone, and Morrison and Wasatch shales are represented in the study areas.

The study sites were about one-quarter acre in size. Boundaries of the brush stands on each site were sketched on graph paper and two rectangular plots, 6 feet by 10 feet, were then located at random in the brush. On these plots, all oak stems one-half inch or larger in diameter were counted to permit comparisons of the density and spacing of stems on different soils and in different types of stands.

Age class distribution and evidence of spread were investigated by means of modified belt transects 5 feet wide and about 100 feet long. These extended completely across small oak stands and 100 feet inward from the edge of large stands. Transects were paired in the form of a cross, one transect lying parallel to the slope and the other on the contour. The center line of each transect was marked by a steel tape, then the oak stem nearest each 5-foot mark was cut and its age determined by ring count. In order to be considered, the stems had to be within 2.5 feet of the designated point on the tape.

The distribution of age classes and location of stems of various ages were used to ascertain what changes, if any, have occurred in the extent and density of oak cover. As supporting evidence of these possible changes, remnants of previous stands, fire scars, and other signs of disturbance were recorded.

Ground cover on each study site was measured along 4 line transects 10 feet long. Two of these were located at random under oak and two in openings. Because of their small size and number, these transects were inadequate to sample individual sites. Information from them was compiled and analyzed for all oak and all open sites and for different types of oak stands. Transects within oak stands were centered in the same plots that were used to determine the spacing between oak stems.

The ground cover transects were divided into 0.1-foot intervals, and credit was given to the item of ground cover that occupied the greatest portion of each interval. Grass foliage, litter, bare soil, and rock were measured. Foliage densities of broad-leaved plants were not listed as ground cover components.

Adjacent to the lower end of each line transect a 2.5-square-foot plot was established for determining utilization and production of grasses and sedges and for estimating foliage density of major forb species. After ocular estimates of utilization were made, grasses and sedges were clipped at ground level, air dried, and weighed. Production of each species on a given plot was computed as follows:

$$\text{Production} = \frac{\text{herbage remaining}}{\text{100-percent utilization}} \times 100$$

Average production of each species on all plots was computed arithmetically. Average utilization was determined by dividing total herbage remaining by total computed production and subtracting the result (expressed as a percent) from 100.

Approximately half of the study sites were being grazed by sheep alone, a third by cattle, and a sixth by both sheep and cattle. Deer and elk use is variable throughout the study area. Deer browse in most of the brush type year-round,

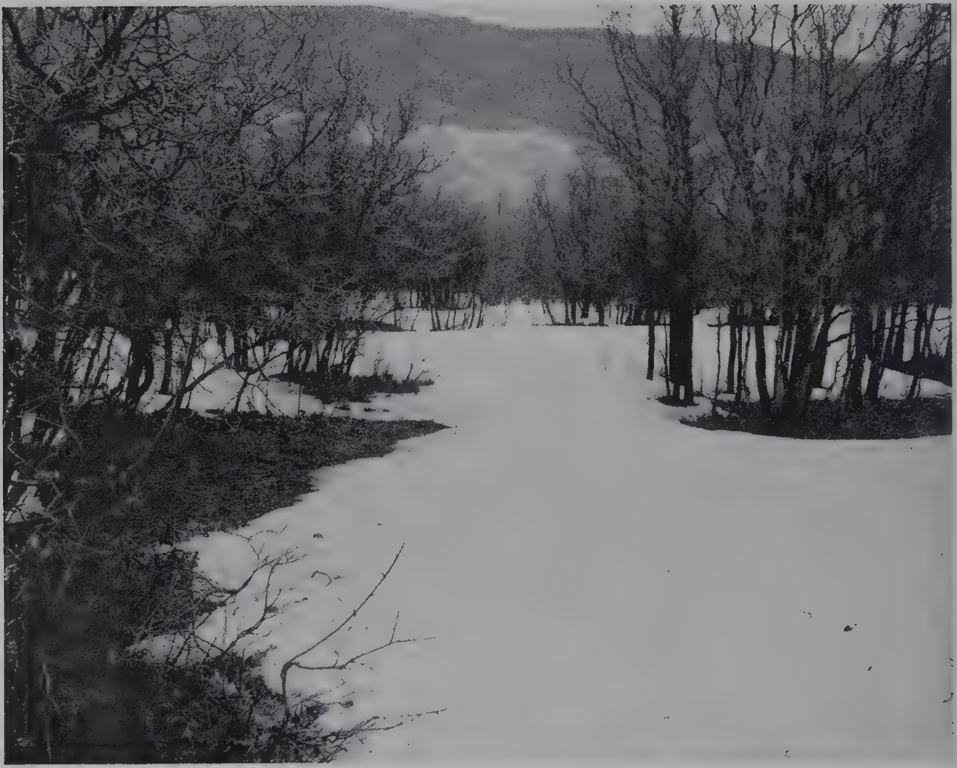

FIG. 2. Gambel oak growing in clumps. This type of stand is found mostly on gentle slopes. Because of its open nature, it offers little restriction to livestock grazing (Cerro Summit, near Montrose, Colorado, March 30, 1954).

whereas elk use is spotty and occurs mostly during the winter months. No attempt was made to record utilization by class of livestock or to distinguish between livestock and big game use.

Erosion and soil stability were evaluated for each transect by using the following classifications suggested by Parker (1951) for the Southwestern Region:

a. Current erosion index, based on soil movement.—Each site was assigned a number between 1 and 15 to denote the relative degree of soil movement. Numbers 13 to 15 indicated little or no evidence of soil movement, with plant and litter cover effective in protecting the soil. Numbers 10 to 12 indicated slight soil movement, which was difficult to recognize. Numbers 7 to 9 indicated moderate soil movement, which was definitely discernible. Movement was often accelerated in some spots and stable elsewhere. Numbers 4 to 6 indicated advanced soil movement, with inadequate protection provided by plant cover and litter. Numbers 0 to 3 indicated severe soil movement, with litter lacking and subsoils often exposed.

b. Erosion hazard index.—This index was used to indicate the proportion of ground surface covered by grass and sedge foliage and by litter. If 90-100% of the transect was covered, an erosion hazard index of 14-15 was assigned; 77-89% cover was indicated by an index of 12-13; 64-76%, 10-11; 50-63%, 8-9; 37-49%, 6-7; 24-36%, 4-5; 10-23%, 2-3; 0-9%, 0-1.

c. Soil stability.—This classification was determined by adding the indices of current erosion and erosion hazard. A total index of 27-30 indicated excellent soil stability; 21-26, good; 15-20, fair; 9-14, poor; 0-8, very poor.

Physical characteristics of the surface soil (A horizon) were determined from observations taken in soil pits near each ground cover transect. On certain sites, samples were taken for pH determinations by the glass electrode method and for phosporus determinations by the sodium bicarbonate method. The evaluations of phosphorus

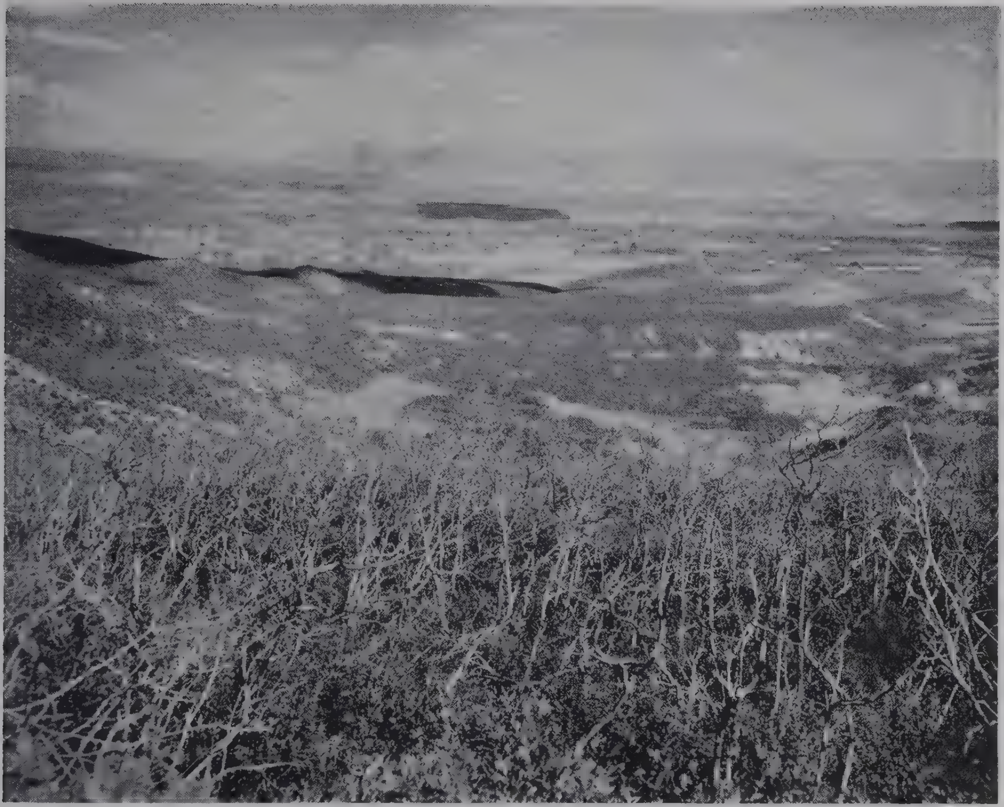

FIG. 3. Gambel oak thickets (foreground) are most common on steep slopes (Grand Mesa, near Delta, Colorado, August 17, 1954).

content are based on the response of wheat, oats and alfalfa to fertilization (Olsen, *et al.* 1954).

GROWTH CHARACTERISTICS OF GAMBEL OAK

Type of Stand

Oak stands were classified according to their size and growth habit into three types: "clump," "thicket," and "intermediate." Small stands less than 100 feet across, usually scattered throughout a grassland or shrub type, were described as clumps (Fig. 2). A thicket was considered to be a nearly continuous stand, usually 5 acres or more in size, which dominated the site and was interspersed with only occasional openings (Fig. 3). Stands larger than clumps but smaller than thickets were classified as an "intermediate" type.

Relationships between type of stand and slope, elevation, and aspect are shown in Table II. The most obvious relationship is that clumps tend to occupy relatively level sites while thickets grow mostly on steep slopes. Clump stands occupy slopes averaging 10 per cent, intermediate stands, 21 per cent, and thickets 31 per cent.

A possible relationship between aspect and type of stand may be noted in the occurrence of clumps only on northerly aspects. Little confidence can be placed in such a relationship, however, because of the relatively small number of clumps sampled and the gentle slopes where they occur.

No consistent relationships were found between type of stand and elevation or soil characteristics.

Effect of Fire and Other Disturbances on Oak Stands

Fire and other disturbances have been responsible for fluctuations in stand density and distribution within the oak brush type. Before describing these effects, however, mention should be made of the reproductive characteristics of Gambel oak. It reproduces most commonly by means of suckers (sprouts growing from surface roots) and stool shoots (sprouts growing from the base of the trunk near the root collar). Reproduction by seed is less evident than vegetative reproduction.

These reproductive characteristics enable

TABLE II. Classification of stands by slope, elevation and aspect

	TYPE OF STAND		
	Clump	Intermediate	Thicket
	No. of stands	No. of stands	No. of stands
Slope (per cent)			
5- 9	3	4	1
10-19	3	5	6
20-29	..	2	5
30-39	..	2	3
40-49	..	3	5
50-54	..	..	4
Elevation (feet)			
7,400-7,499	..	..	4
7,500-7,999	4	3	3
8,000-8,499	2	6	12
8,500-8,999	..	5	3
9,000-9,400	..	2	2
Aspect			
North	3	..	1
Northeast	2	2	2
East	..	5	4
Southeast	..	2	5
South	..	2	3
Southwest	..	..	1
West	..	4	6
Northwest	1	1	2
	6	16	24

Gambel oak to withstand most disturbances and often to increase as a result of them. Fire may kill the above-ground portions of oak plants but it seldom kills the entire plant. The most common effect is to stimulate suckering with resultant thickening of open stands and merging of scattered stands into continuous thickets. A possible explanation for the occurrence of thickets on steep slopes is the tendency for fire on such terrain to spread over larger areas and to burn through the brush more thoroughly than on level ground, thus causing widespread suckering.

Available information shows that herbicides affect oak in nearly the same manner as fire. Cutting, on the other hand, appears to stimulate the development of stool shoots more than suckers. The effects of repeated burning, spraying and cutting are not known.

Age, Size and Density of Oak

About half the 2,000 Gambel oak stems observed were in the 0-9 year age class. Each of the other age classes contained less than 10 percent of the total, on the basis of average values for all stands (Table III).

Stems over 100 years of age were scarce, comprising only one percent of the total stand; however, they were rather uniformly distributed throughout the study area. The oldest stem on which an accurate ring count could be made was 212 years of age.

TABLE III. Age class distribution of Gambel Oak

Age Class	Date of establishment	Average for all Stands[1]	TYPE OF STAND[2]			STAND CONDITION[3]	
			Clump	Intermediate	Thicket	Disturbed	Undisturbed
Years:		%	%	%	%	%	%
0- 9	1945-54	50	58	48	47	48	41
10- 19	1935-44	10	9	11	9	13	7
20- 29	1925-34	5	2	5	7	8	2
30- 39	1915-24	7	1	7	9	8	4
40- 49	1905-14	5	2	6	5	5	4
50- 59	1895-1904	5	5	6	4	5	7
60- 69	1885-94	8	10	8	7	6	14
70- 79	1875-84	7	10	5	8	5	15
80- 89	1865-74	2	3	1	3	1	4
90- 99	1855-64	0.4	0	0	1	0	1
100-199	1755-1854	1	0	3	0.1	1	1
		100.4	100	100	100.1	100	100

[1] Based on 47 sites, 45 of which were in oak stands and 2 of which were in openings where oak reproduction was encroaching.

[2] Based on 46 oak sites, 6 of which were clump type, 16 intermediate type, and 24 thicket type.

[3] Based on 36 oak sites (25 disturbed and 11 undisturbed).

The only obvious relationship observed between age-class distribution and type of stand was a scarcity of 20-49-year-old stems in the clumps. This may be explained by the fact that very few fires have burned through the clumps in recent years. If fires had been more frequent on these sites, the clumps would probably have merged and become indistinguishable. The presence of more 100-199-year-old stems in intermediate stands than in clumps or thickets may be significant; however, these old trees are so scarce as to make such an interpretation hazardous.

The size of Gambel oak is often influenced by the depth of surface soil. On favorable sites with a surface soil deeper than 12 inches the species may attain a tree-like form, with a diameter of 3 to 5 inches and a height of 10 to 20 feet. On surface soils of 5 inches or less, mature stems are usually between 2 and 3 inches in diameter and less than 10 feet high. The largest Gambel oak observed was 28 inches in diameter at stump height and about 30 feet high.

The density of oak brush is affected by age of the stand, characteristics of the site, and past history. When first established, especially following fire or cutting, the young stand may form an impenetrable thicket. In one stand of this sort, which was between 20 and 30 years old, stems 0.5 inch or larger in diameter were only 12 inches apart on the average. As the stands mature they thin out, often to the point where the larger stems are 3 to 6 feet apart. This is especially true on sites where the soil is deep; on soils with an A horizon deeper than 17 inches the spacing between stems was twice as great as on shallower soils.

Ordinarily, stems grow closer together in thickets than in clumps. Stems have an average spacing in thickets of about 2 feet compared with 3 feet in clumps.

Evidence Regarding Spread

The historical evidence that extensive oak stands have existed for a long period is supported by findings of the present study. On at least 89 percent of the study sites, oaks were growing at the time of the first real settlement of west-central Colorado in 1880, and the remaining sites are within a short distance of stands known to date back to that time. On about two-thirds of the study sites, long-dead stumps and fallen trees were found. This indicates the existence of an oak cover before the present stand was established.

In addition to having been in existence for a long time, most of the oak stands studied evidently have not spread a great deal in recent years. In a spreading stand, one would expect to find the oldest stems near the center, with younger stems toward the perimeter, and reproduction encroaching in the openings between stands. These conditions were found only occasionally. In most oak stands the distribution of stems of various ages followed no set pattern and there was an abrupt transition between the oak stands and adjacent openings. Oak reproduction did not occur at all in half of the openings between stands, and where it was observed its foliage usually covered less than 20 percent of the openings.

Another indication that the oak brush type has not gone through any periods of drastic spread lies in the fact that except for the youngest class no single age class or group of age classes was predominant over a large number of sites (Table III). The larger proportion of oaks less than 10 years old is not believed to be an indicator of current spread; it seems to be a normal situation because these young oaks are common even in undisturbed stands. The apparently high proportion of stems established between 1875 and 1894 is of doubtful significance and is probably due to sampling.

The age class distribtuion also shows a scarcity of oaks older than 79 years. This is likely the result of natural mortality, as annual ring counts on dead oaks show that most trees die before reaching an age of 80 years. By similar reasoning, the increase in the number of stems younger than 79 years can more logically be considered part of a natural distribution pattern than an indication of spread.

Signs of fire, cutting, and herbicide treatment, all of which seem to be conducive to thickening, were found on about two-thirds of the study sites (Table III). On these recently disturbed sites the proportion of younger age classes was higher than on the undisturbed sites, apparently as a result of the disturbance. The relative scarcity of stems older than 59 years in disturbed stands may be due to the killing of those stems by the same fire or cutting which left the scars observed during the study. The relatively high proportion of 60-79-year-old stems in undisturbed stands proved to be significant at the 5 percent level; however, the data are based on only eleven sampling units and the sampling error was 50 percent, making a weak basis for interpretation.

The effect of fire in thickening an oak stand is apparent from observations on recently burned areas. Reproduction has sprung up in profusion and within 2 or 3 years formed a solid canopy (Fig. 4). The appearance of suckers after a single fire is limited to the lateral extent of surface roots; therefore appreciable marginal extension of a stand cannot be expected. However, recurrent fires over a long period might well result in thickening and joining of scattered stands.

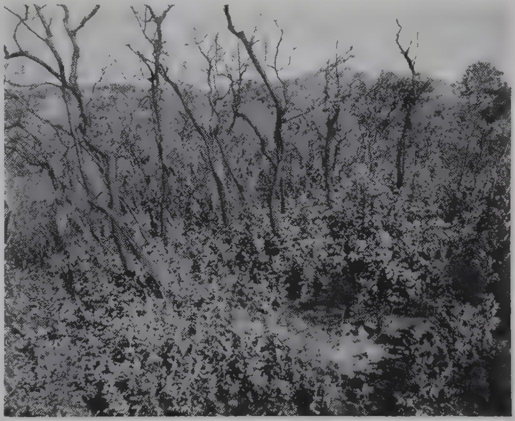

Fig. 4. Dense growth of oak reproduction 3 years after burning (Dewey Nurrell ranch near Collbran, Colorado, September 22, 1953).

While it appears likely that disturbed stands have thickened to varying degrees on the study areas, it does not necessarily follow that the type as a whole is thicker or more extensive than it was 75 years ago. Even though some stands have thickened, others have become thinner with age. The most tenable concept of spread of oak brush is that it tends to thicken and spread under disturbance and to thin out or retreat when protected from fire and cutting. Over a period of time these influences have tended to counterbalance one another.

Natural Enemies of Gambel Oak

The only important natural enemy of oak observed in 1953 and 1954 was a defoliator tentatively identified as *Lambdina punctata* (Hulst.). This looper infested about 2,500 acres of oak brush in the vicinity of Ridgway and completely defoliated many stands. The insect showed a strong preference for oak and made relatively little use of associated vegetation.

It is doubtful that a single defoliation seriously damages an oak stand; however, infestations that persist for several years appear to be capable of killing the stems. Local residents recall a 2-year infestation during the early 1930's that killed the oak over extensive areas. Examination of these areas in 1954 showed numerous snags surrounded by variable densities of young oak, apparently established shortly after the infestation. The oak kill here can hardly be attributed to drought as the monthly and annual precipitation at nearby stations during the early 1930's was not markedly deficient.

Comparison of Ground Cover under Oak and in Openings

The ground cover under oak differs considerably from that in openings, especially where the oak stands are dense and continuous. In general, the oak ground cover is characterized by a continuous layer of leaf litter, a predominance of sedge, and relatively few forbs. The openings typically have more bare soil exposed and less litter. Composition of the plant cover in openings tends to be more variable than in oak stands.

Besides Gambel oak the most common shrubs observed in the oak brush type are: snowberry (*Symphoricarpos oreophilus* Gray), big sagebrush (*Artemisia tridentata* Nutt.), serviceberry (*Amelanchier alnifolia* Nutt.), chokecherry (*Prunus virginiana* L.), and rose (*Rosa* spp.). All of these species grow both under oak and in openings.

Elk sedge (*Carex geyeri* Boott.) is by far the most common of the grass and grasslike plants under oak, while Kentucky bluegrass (*Poa pratensis* L.) predominates in the openings. Other grasses present, mainly in the openings, are bluestem wheatgrass (*Agropyron smithii* Rydb.), Letterman needlegrass (*Stipa lettermanii* Vasey), and Thurber fescue (*Festuca thurberi* Vasey).

In order of their abundance the most common forbs in the oak brush type are daisy (*Erigeron* spp.), western yarrow (*Achillea lanulosa* Nutt.), vetch (*Vicia americana* Muhl.), knotweed (*Polygonum douglasii* Greene), and lupine (*Lupinus* spp.). Daisy and knotweed are most common on open sites, whereas vetch occurs mostly under oak. Forbs are usually more abundant in the openings than under oak.

To provide a basis for comparing composition of oak stands in western Colorado with that in other areas the frequency of plant species in different types of stands is shown in Table IV.

Table IV. Frequency of occurrence of species in oak stands

Species	Type of Stands Clump	 Intermediate	 Thicket	Average
	Per cent	Per cent	Per cent	Per cent
WOODY PLANTS				
Quercus gambellii Nutt.	100	100	100	100
Symphoricarpos oreophilus Gray	75	88	61	71
Rosa spp.	8	17	20	17
Amelanchier alnifolia Nutt.	17	12	17	16
Prunus virginiana L.	25	12	9	12
Artemisia tridentata Nutt.	17	8	4	7
Ribes spp.	...	...	4	2
Rubus sp.	8	...	...	1
Chrysothamnus spp.	8	...	...	1
GRASS AND GRASSLIKE PLANTS				
Carex geyeri Boott.	92	42	50	54
Poa pratensis L.	67	33	30	37
Agropyron smithii Rydb.	8	54	28	33
Stipa lettermanii Vasey	25	21	13	17
Bromus anomalus Rupr.	25	8	7	10
Koeleria cristata L. Pers.	17	...	9	7
Festuca thurberi Vasey	...	12	4	6
Stipa spp.	...	...	9	5
Horaeum sp.	...	...	2	1
Sitanion hystrix Nutt.	...	...	2	1
Phleum pratense L.	...	...	2	1
Unknown species	8	21	9	12
FORBS				
Achillea lanulosa Nutt.	42	67	46	51
Vicia americana Muhl.	33	17	30	27
Wyethia spp.	8	4	11	9
Pulsatilla ludoviciana Nutt.	...	12	8	9
Aster spp.	...	8	9	7
Erigeron spp.	8	4	7	6
Taraxacum officinale Wiggars	17	8	2	6
Polygonum douglasii Greene	...	17	...	5
Thalictrum spp.	17	4	2	5
Lupinus spp.	8	...	4	4
Viguiera multiflora (Nutt.) Blake	...	...	7	4
Potentilla spp.	...	4	2	2
Astragalus spp.	17	...	...	2
Berberis repens Lindl.	...	4	2	2
Geranium sp.	...	...	2	1
Fragaria spp.	...	4	...	1
Unknown species	...	...	4	2

By frequency is meant the percentage of the total number of sampling units in which a species occurred. There were 12 sampling units in clumps, 24 in intermediate stands and 46 in thickets—a total of 82 units. A complete record was kept of woody species and grasses on each unit; however, the list of forbs is based only on the major species present.

Because of the small size and limited number of sampling units in each type of stand the differences in composition between stand types cannot be considered meaningful unless they are of relatively large magnitude. With this in mind the differences between the three stand types might be summarized as follow: (1) woody plants and forbs: no major differences; (2) grass and grasslike plants: greater frequency of *Carex* and *Poa* in clumps; lower frequency of *Agropyron* in clumps.

Average areal extent of the various ground cover components is shown in Table V.

TABLE V. Comparison of plant and ground cover under oak and in openings[1]

Kind of cover	Under oak	In openings
	Per cent	Per cent
Grass and sedge	23	20
Litter	72	48
Rock	1	4
Bare soil	4	28
	100	100

[1] Based on transect measurements. Forbs were not measured on these transects.

In reference to Table VI, total production of grasses and sedges, which averaged 346 pounds per acre, was substantially the same under oak and in the openings. However, production of individual species differed considerably. The data showed no consistent relationship between type of stand and total grass and sedge production.

TABLE VI. Average production of grasses and sedges under oak and in openings

Species	Under oak	In openings
	lbs./acre	lbs./acre
Elk sedge	204	25
Kentucky bluegrass	52	137
Letterman needlegrass	18	54
Bluestem wheatgrass	11	66
Minor species	38	86
Total	323	368

Precipitation and other climatic factors influencing production were about normal during the 1953 growing season when these measurements were made.

Grasses were grazed more closely in openings than under oak (Table VII). However, sedge received much greater use under oak than in openings, thereby making the overall difference in utilization between oak and openings nonsignificant. These data cannot be used to judge the degree to which oak brush restricts livestock grazing because no distinction was made between livestock and game use. Possibly other animals were responsible for the use under oak.

There were no consistent differences in the degree of utilization of grass and sedge in clumps, thickets, or intermediate stands.

TABLE VII. Average utilization of grasses and sedges under oak and in openings

Species	Under oak	In openings
	Per cent	Per cent
Elk sedge	22	8
Kentucky bluegrass	17	49
Letterman needlegrass	4	40
Bluestem wheatgrass	10	16
Minor species	5	8
All species	18	29

No data were collected on production or utilization of woody plants or forbs.

COMPARISON OF SOIL UNDER OAK AND IN OPENINGS

Color, texture, consistency, and stoniness of the surface soil (A horizon) were found to be essentially the same in the openings as under oak stands.

Depth of the A horizon varied with slope and kind of cover present. On slopes of 0-39 per cent, the A horizon was 16 in. deep under oak and 21 in. under openings. On slopes of 40 per cent and more, this horizon was 18 in. deep under oak and 13 in. at openings.

The relationship between soil depth and oak brush cover is not apparent from a comparison of average depth for all slopes under oak and in openings. However, it does appear when the plots are stratified into two slope classes.

Depth of the A horizon under oak is about the same on steep slopes as on gentle slopes, averaging 17 inches. In the openings, on the other hand, it is definitely shallower on steep slopes. A comparison of soil depths by slope classes under oak and in the openings shows that on gentle slopes the A horizon is consistently deeper in the openings; on steep slopes it is more variable, but tends to be deeper under oak.

Most surface soils are dark brown, with textures varying from fine sandy loam where derived from Dakota standstone to clay where derived from Mancos shale. Although no consistent differences between the stoniness of soil under oak and in the open were noted, stoniness was influenced by soil origin. Most noticeable was the relative scarcity of stones in soils derived from the the Wasatch formation.

Consistency of the soil was the same under oak and in openings on three-fourths of the sites. On the remaining areas the soil was looser under oak than in openings.

Soil reaction was favorable for plant growth on most sites. Soils in openings had a consistently higher pH than those under oak—an average of 6.6 compared with 6.3.

Available phosphorus content of the A horizon varied from 0 to 245 pounds per acre. Of the 19 soils tested, 13 had less than 50 pounds of P_2O_5 per acre. This deficiency indicates that these soils would probably respond to fertilization. Six had more than 50 pounds per acre, indicating little likelihood of response to fertilization. There was no consistent difference in the phosphorus content of soils in oak stands and those in the open.

Because Gambel oak was common on all soils in the study areas, it appears doubtful that its distribution is limited to a great extent by soil factors.

No soil classification data have been published for soils in the oak brush type of west-central Colorado.

SOIL EROSION

The proportions of oak and open sites in the various erosion classes are shown in Table VIII.

TABLE VIII. Classification of erosion on oak and open sites

Erosion Classification	PROPORTION OF TOTAL PLOTS IN EACH EROSION CLASS	
	Oak	Open
	Per cent	Per cent
Current Erosion Index (Soil movement)		
None	62	6
Slight	36	22
Moderate	1	37
Advanced	..	28
Severe	1	7
Erosion Hazard Index (Percent grass, sedge and litter)		
90-100	83	21
77- 89	15	20
64- 76	1	21
50- 63	1	13
37- 49	..	11
24- 36	..	8
10- 23	..	6
0- 9	..	..
Soil Stability Classification		
Excellent	68	7
Good	31	28
Fair	..	35
Poor	1	21
Very poor	..	9

Under oak, the plant and litter cover is usually very effective in protecting the soil from erosion. Pocket gophers, which seem to prefer oak sites to open ones, were responsible for the limited soil movement observed.

The current erosion index under oak averaged 13, indicating little if any soil movement. The average ground cover density of litter, grass and sedge was 95 per cent; erosion hazard index was 14. This value, added to the current erosion index, resulted in an average soil stability classification of 27, which is considered excellent.

Current erosion in the openings was almost always more severe than under oak. An average index of 8 was recorded for openings, indicating moderate soil movement. Average ground cover density of litter, grass, and sedge in the openings was 68 per cent, or an erosion hazard index of 10. Added to the current erosion index, this gives a soil stability classification of 18, which is described by Parker as "fair."

SUMMARY AND CONCLUSIONS

The oak brush type in west-central Colorado was investigated in 1953 and 1954 to learn some of the charatceristics of oak brush and its environment and to find out whether oak brush is spreading or has spread in recent years.

Oak brush comprises a major portion of the vegetation between 7,000 and 9,000 feet in the study area. On gentle slopes, it usually grows in clumps, while on the steeper slopes it more commonly occurs in thickets.

About half the oak stems in a normal stand are less than 10 years old. The remainder are distributed rather uniformly throughout the 10-to-80-year-old age classes. Stems older than 80 years are relatively scarce, indicating a natural early mortality. The average mature stem is about 13 feet high and 3 inches in diameter.

Oak stands are most dense when young, especially following a fire or other disturbance that stimulates reproduction. As the stands mature, they become thinner.

The total production of grass and sedge, which averaged 346 pounds per acre on all sites, was similar under oak and in openings. Elk sedge was the dominant herbaceous plant under oak, and Kentucky bluegrass was predominant in the openings.

Utilization of grass and sedge averaged 24 percent on all sites. Grass was utilized more closely in openings while sedge was used more heavily under oak.

Although characteristics of the surface soil are quite variable, soil factors do not appear to limit the distribution of oak brush. Under oak, depth of the A horizon was fairly uniform regardless of slope; whereas in openings it averaged 8 inches shallower on steep slopes than on gentle slopes.

Average depth of the A horizon on all sites was 18 inches.

Soil stability was rated as "excellent" under oak and "fair" in the openings. The average ground cover index under oak was 95 percent compared with 68 percent in the openings. Moderate soil movement was evident in the openings, but little or none was observed under oak.

Very few of the oak stands observed in 1953 and 1954 appeared to be spreading, as evidenced by the scarcity of reproduction in the openings between stands. Although some stands have thickened in recent years, usually as a result of fire, others have become thinner. Consequently, the general extent and density of the type is probably not greatly different today than it was in the late 1800's.

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AN ANALYSIS OF A WOOLGRASS (*SCIRPUS CYPERINUS*) COMMUNITY IN WISCONSIN

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INTRODUCTION

During the last two weeks of August, 1951, I had occasion while an employee of the U. S. Fish and Wildlife Service[1] to survey the vegetation of two marshes in central Wisconsin by means of permanent belt transects. The striking feature of these marshes was the presence of woolgrass, *Scirpus cyperinus* (L.) Kunth, in extensive stands apparently occupying a place in the ecological structure of the area similar to that usually occupied by cattail (*Typha* spp.) in other areas. In order to determine the true extent of similarity, an analysis of one of the woolgrass communities was undertaken.

DESCRIPTION AND LOCATION OF THE WOOLGRASS MARSH

Rynearson Pool No. 2, the woolgrass area, is located on the Necedah National Wildlife Refuge in Juneau County in central Wisconsin. It occupies parts of Sec. 31 and 32, T19N, R3E and Sec. 5 and 6, T18N, R3E.

The topography of the drainage basin is that of the gently undulating bed of Glacial Lake Wisconsin (Martin and Krefting, 1953). Many marshy areas are interspersed between sandy ridges and islands. The watershed is mostly forested, with stands of jack pine (*Pinus banksiana* Lamb.) and oak (*Quercus* spp. L.) predominating. Stands of aspen (*Populus tremuloides* Michx.) are also common.

The natural stream drainage of the area is very poor, but a system of open drainage ditches, left from an attempt at agricultural reclamation during the period 1900 to 1920, provides an adequate supply of water to the marsh at all seasons except during drought years. The area drained, as delineated by these ditches, is about 45 square miles.

The marsh itself is the result of an artificial impoundment created in 1939. Due to the extremely low relief of the bottoms, an area of about 650 acres is impounded with depths exceeding six feet only in the vicinity of dikes and in the abandoned drainage ditches. The bottom is predominantly firm sand, but accumulations of or-

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[1] The author wishes to thank the U. S. Fish and Wildlife Service for permission to use the data presented here.

ganic matter occur in some areas, especially in stands of emergent vegetation. The water is near neutral and has a carbonate content of about 32 ppm (Zimmerman 1943).

HISTORY

Originally this area was vegetated by red pine (*Pinus resinosa* Ait.) and white pine (*Pinus strobus* L.) on the islands and ridges, with spruce-tamarack (*Picea mariana* (Mill.) BSP-*Larix laricina* (DuRoi) K. Koch) bogs occupying the low areas (Grange 1948). Settlement commenced about 1855 and logging of the pineries was in full swing about 1880. A distastrous fire in 1893 eliminated most of the tamarack and spruce in the bogs. Following this fire, the country became very prairie-like with a few scattered oaks and pines on the islands. Many of the former bog areas developed extensive stands of wire-grass (*Spartina pectinata* Link). Between 1893 and 1900 fires were common and widespread.

Drainage and settlement proceeded apace in the decade 1900-1910. In 1910 a fire again burned large acreages of wild lands. Around 1920 the last drainage ditches were dug. Agricultural depression, excessive drainage district taxes, and drought caused extensive abandonment of farms by 1925.

In the fall of 1930 occurred the most extensive fire in the history of the area. It burned huge holes in the bog peat and is reported to have denuded the humus and topsoil from most of the sand ridges and islands (Grange 1948).

From the records of the Necedah Refuge it is known that the area which is now the woolgrass marsh was farmed as late as 1936. Flooding of the marsh occurred in 1939. A water level management program was instituted on the study area in 1946. This program has called for lowering water levels approximately three feet from early June to mid-September on alternate years. Thus, about one third to one half the area was drained of surface water during the summers of 1946, 1948, and 1950.

METHODS AND TECHNIQUES

The five transects from which data were obtained were established in 1950. They were marked at both ends, and at intermediate positions on very long transects, by steel fence posts painted yellow. Established systematically, they were three feet wide and had a total length of 22,199 feet. Although data were gathered originally for the entire length of each transect, portions traversing upland or open water areas have been eliminated as irrelevant to this study. *Scirpus cyperinus* (L.) Kunth was present in varying amounts on about 4,575 feet of the five transects; and it is with this sample that we are concerned.

In order to facilitate gathering this large quantity of data in the limited time available, I developed the following technique in recording vegetation. First, with the use of hand compass and steel surveyor's tape, 100 feet was chained along the transect line. Then the vegetation growing along the tape was divided into relatively homogeneous units on the basis of physiognomy. The lengths of these units were recorded in sequence and the species of plants and their abundance within each unit recorded. Abundance was estimated as dense, medium, light, scattered, and trace. Such ratings were usually based on per cent of coverage, but in non-leafy species such as *Eleocharis acicularis* (L.) R & S, stem density was used. For convenience in tabulation, numerical values were assigned to these density or per cent coverage classes as follows:

+ Trace or no cover value
1 scattered or 1 to 25 per cent coverage
2 light or 26 to 50 per cent coverage
3 medium or 51 to 75 per cent coverage
4 dense or 76 to 100 per cent coverage

Woolgrass stands occurred on the transects 35 times. Table I lists these stands, the species which occurred in them and their cover value, water depth, and presence or absence of transitions to upland or submergent communities. Since these stands sometimes contained more than one of the units recorded in the field, in some cases the cover values in Table I represent a value weighted by the extent of occurrence within the stand. Thus a species with an abundance rating of 4 but occurring only in one-half the sample was given a value of 2 for the entire sample.

The symbols used to indicate presence or absence of transitions are as follows: + present, 0 absent, and — not applicable; either no upland or open water adjacent.

RESULTS AND DISCUSSION

Since the original data were recorded in units of similar gross appearance, it seemed useful to employ these data for a more detailed analysis of the structure of the woolgrass community. Inspection of field data indicated that three sub-communities might be recognized on the basis of dominance in the lower strata. These were named the woolgrass-sedge, woolgrass-grass, and woolgrass-spikerush sub-communities. Table II shows the per cent frequency of occurrence of the various species in the units placed in these sub-communities. Also indicated are average water depths and the number of species for each sub-community.

TABLE I. Cover, water depth, and transitions in thirty-five stand samples of woolgrass, Rynearson Pool No. 2, Necedah Wildlife Refuge, Juneau County, Wisconsin. (+ = trace coverage; 1 = 1-25% coverage; 2 = 26-50% coverage; 3 = 51-75% coverage; 4 = 76-100% coverage)

Stand number	Length of transect in sample (feet)	Water depth in inches	Upland transition	Submergent transition	*Scirpus cyperinus*	*Carex* sp.	*Glyceria borealis*	*Phalaris canariensis*	*Spirea alba*	*Salix* sp.	*Polygonum* sp.	*Sagittaria latifolia*	*Lemna minor*	*Eleocharis obtusa*	*Eleocharis acicularis*	*Scirpus validus*	*Leersia oryzoides*	*Juncus* sp.	*Typha latifolia*	Algae	*Iris versicolor*	*Potamogeton foliosus*	*Elodea canadensis*	*Alisma triviale*	*Spartina pectinata*	*Sparganium chlorocarpum*	*Potamogeton pusillus*	*Rumex* sp.
1	200	0- 1	+	0	4	1												1										
2	85	1-15	0	0	3	3			+	1			1	+	2						1			1				
3	134	3-12	+	0	3	3	2						+		1													
4	23	1- 8	+	0	3	3																						
5	50	6-15	0	0	3	2	1						+															
6	124	1- 6	+	—	3	4	1			1									1									
7	49	1- 6	0	—	4	1	1					1							1									1
8	55	0- 6	+	—	4	3																						
9	126	1-18	+	0	2	2																						
10	104	1-15	+	—	4	2					1	1																
11	28	0- 1	0	0	3	1											1	1										
12	87	0- 1	0	0	3	2																						
13	850	12-15	0	0	3	3																						
14	34	0 -3	+	0	4	1					1					+		1										
15	116	3-10	—	+	3		2	+	1	1						1												
16	37	1- 3	0	—	1		3		1						1			+			1			1				
17	400	12-15	+	0	4			1						1	1								1					
18	128	0- 1	+	—	1			4																				
19	264	6-18	+	—	4			1					+				1			2		1	1			1		
20	45	3-16	0	0	2				1	1	2		2						1						2			
21	100	0- 1	—	+	2		1					1																
22	70	0- 8	+	+	3		1		1	1		1		2		2												
23	104	1-12	+	0	3		2		1		1	1		1		+	1											
24	80	6-15	+	—	3					+		1	+			+			1									
25	16	6-18	0	0	3							+	+															
26	73	6-18	—	0	3							1																
27	64	3-12	+	—	1		1					1	+			1	1	+		1		1	1					
28	34	0-12	0	—	1							1		1	1						+							
29	21	1- 8	0	0	3							1			2	+												
30	50	0- 6	+	0	2	2						1		2		1	1											
31	130	15-22	—	0	1	1								1	2					1		1						
32	8	3- 6	+	0	1	1		1										4										
33	58	3-15	+	0	2	1	1						1	1		1		2										
34	33	0- 1	0	—	1	2												4										
35	86	12-15	0	0	4								4			+	1	1		2							1	

On the basis of Table II it becomes apparent that three types of woolgrass stands may definitely be recognized. These appear to be closely related to water depth. There is, however, considerable overlap in the range of water depths occupied. It is therefore doubtful if water depth is the sole cause of the distinction between sub-communities. The species of plants characteristic of these stands reflect differences in average depths quite closely, however.

Woolgrass-sedge type

This sub-community occurred 13 times on the transects. Over 60% of the stands of woolgrass with a coverage of 75-100 per cent occurred in this type. The average coverage of woolgrass in these stands was over 50 per cent. *Carex* spp. also showed a high degree of cover dominance, averaging over 50%. As a result of the intense competition of these species, subordinate species were few in number, infrequent in occurrence, and exhibited an average cover value of less than 1.

Woolgrass-grass type

This sub-community occupied the shallowest water of the three types. It was often associated with a transition to dry land. The average cover

TABLE II. Frequency of occurrence, number of species, and average water depth of three woolgrass sub-communities, Rynearson Pool No. 2, Necedah Wildlife Refuge, Juneau County, Wisconsin

	Woolgrass-Grass	Woolgrass-Sedge	Woolgrass-Spikerush
Number of samples	13	22	20
Average water depth (inches)	3.7	5.2	7.9
Range of water depth (inches)	0-18	0-18	0-22
Frequency of occurrence (%)			
Scirpus cyperinus (L.) Kunth	100	100	100
Carex sp. L.	7.7	86.3	.....
Glyceria borealis (Nash) Batchelder	46.2	8.2	15.0
Phalaris canariensis L.	38.5	.....	10.0
Spirea alba DuRoi	38.5	4.5	. .
Salix sp. L.	30.8	9.1	5.0
Polygonum sp. L.	23.1	4.5	
Sagittaria latifolia Willd.	.....	4.5	50.0
Lemna minor L.	15.4	9.1	25.0
Eleocharis obtusa (Willd.) Schultes	7.7	4.5	40.0
Eleocharis acicularis (L.) R & S	15.4	.....	25.0
Scirpus validus Vahl	15.4	4.5	35.0
Leersia oryzoides (L.) Sw.	15.4	4.5	20.0
Juncus sp. L.	7.7	13.6	30.0
Typha latifolia L.	7.7	9.1	5.0
Algae	7.7	.....	15.0
Iris versicolor L.	15.4	4.5	5.0
Potamogeton foliosus Raf.	7.7	.....	10.0
Elodea canadensis Michx.	15.4	.....	5.0
Alisma triviale Pursh	7.7	4.5	.....
Spartina pectinata Link	7.7	.....	.....
Sparganium chlorocarpum Rydb.	7.7	.....	.....
Potamogeton pusillus L.	.....	.....	5.0
Rumex sp. L.		4.5	. .
Naias flexilus (Willd.) Rostk. & Schmidt	.	.....	5.0
Total number of species	21	16	18

of woolgrass in this type is between 26 per cent and 50 per cent. A group of species is highly characteristic of this sub-community. These are *Glyceria borealis* (Nash) Batchelder, *Phalaris canariensis* L., *Spirea alba* DuRoi, *Salix* spp., and *Polygonum* spp. and all are characteristic of moist soil or shallow water. The frequency of occurrence of these species ranges from 23.1 per cent for Polygonum to 46.2 per cent for *Glyceria borealis*. The average cover value of this group is 2.

Since the combined cover of the characteristic species of this sub-community is usually high, other species occur only infrequently and at low cover values. However, the somewhat drier habitat permits a greater variety of such species.

Woolgrass-spikerush type

This is the deepest water sub-community. The average cover value of woolgrass in this type is also 2 or 26-50 per cent. *Sagittaria latifolia* (Willd.), *Eleocharis obtusa* (Willd.) Schultes, *E. acicularis* (L.) R & S, *Scirpus validus* Vahl, *Leersia oryzoides* (L.) Sw., and *Juncus* spp. all occur much more frequently in this type than in the others. *Lemna minor* L. might possibly be included, but it occurs in only slightly lower frequencies in the other types. The average cover of each of these species is quite low, less than 25 per cent.

Two species occurred only in this sub-community. These are *Naias flexilus* (Willd.) Rostk. & Schmidt and *Potamogeton pusillus* L. However, each occurred in only one sample and probably represent accidentals from adjacent submergent communities. In general, the minor species in this type were of the submergent growth form.

Relationships between sub-communities

Upon examination of the geographic location of the samples of these types, a distinct pattern was apparent. Most striking was the location of all the woolgrass-sedge sub-communities in the upper ⅖ of the marsh, to the virtual exclusion of the other types. This seemed to be related to very low bottom gradients, resulting in large areas favorable for this type. The sequence of sampling also indicated a gradual shift in dominance from woolgrass to sedge as drier land was approached. In some instances this resulted in a pure stand of sedge (*Carex* spp.) before dry land was reached.

In the lower ⅗ of the marsh no stands of the woolgrass-sedge type occurred on the transects. In general, the woolgrass stands in this area were much narrower, as shown by shorter transect samples traversing them. This seems to reflect slightly steeper shore areas with a narrower band of water depths suitable for emergent growth in this portion of the marsh. As would be expected, the woolgrass-grass stands usually occupied the shallower areas of this zone. Exceptions were found, however. In these instances, the woolgrass-grass type was found in nearly the maximum depth of water that woolgrass will tolerate—about 18 to 20 inches. These stands often show only one of the characteristic grasses of this type, usually with a very low cover value. This probably represents a disturbance community resulting from summer water level draw-downs.

From the preceding discussion, it appears likely that two forms of community succession occur in this marsh, depending on variations of bottom gradient. In areas of low bottom gradient, the succession may be diagrammed as follows:

$$\text{Submergent} \longrightarrow \begin{array}{c}\text{Woolgrass}\\ \text{Spikerush}\end{array} \longrightarrow \begin{array}{c}\text{Woolgrass}\\ \text{Sedge}\end{array} \longrightarrow \text{Sedge} \longrightarrow \text{Upland}$$

Many variations from this pattern occur. The submergent and woolgrass-spikerush stages frequently were not encountered between upland areas. Also, the sedge stage was frequently not a pure stand but was mixed with some woolgrass.

For the succession in areas of steeper, but still very gentle, bottom gradients, the following diagrammatic picture seems most typical:

$$\text{Submergent} \longrightarrow \begin{array}{c}\text{Woolgrass}\\ \text{Spikerush}\end{array} \longrightarrow \begin{array}{c}\text{Woolgrass}\\ \text{Grass}\end{array} \longrightarrow \text{Upland}$$

Again, many variations of all possible types occur.

Presence of transitions

The stands considered in Table I were also examined, via field notes, for the presence or absence of transition zones, with the results indicated in that table. This was done in order to determine, as far as possible, how discrete the woolgrass communities were. In general, transitions were absent between the woolgrass community and the submergent community, indicating that the woolgrass stands were sharply delineated at their outer edge. Eighteen of the 31 stands adjacent to upland showed a transition. Thus, considerable overlap of species occurs on the upland side of the woolgrass stands.

Ecological position of woolgrass

The list of plant species found associated with woolgrass in this study is typical also of stands of cattail (Segadas-Vianna 1951, and unpublished studies of the author). Even the sub-assemblages discerned and cover values involved are similar. The range of water depths, the soil type, and water quality occupied by woolgrass are well within the wide range of sites occupied by cattail stands. Thus, it appears that woolgrass and cattail are probably very close ecological relatives.

This poses the very interesting question of why woolgrass should dominate to the virtual exclusion of cattail in the marsh studied. Cattail was present (Table I), but only in insignificant amounts. It was apparently unable to compete successfully with the woolgrass in this marsh. The occurrence of cattail stands in similar nearby areas indicates that the fire history of the general vicinity was not the factor which has prevented cattail dominance. The most probable explanation at present seems to be that the history of water level fluctuations has been more favorable for woolgrass than cattail. At least no other factor in the ecology of the woolgrass marsh appears sufficiently different from that of cattail marshes to account for the difference.

If this is the case, it must be pattern, or chronology of water level fluctuation that is important, since cattail is also found in areas of fluctuating water levels. The pattern of water level fluctuation found normally due to natural causes is quite different from that found in the woolgrass marsh. In the normal pattern high water levels prevail in spring and early summer, followed by a gradual decrease to a late summer or early fall minimum. In contrast, in the study area, water levels were drawn down about three feet by late June on alternate years. They were held there until mid-September when they were gradually raised so that normal or full pool levels were attained before freeze-up. Thus, it is possible that this pattern of water level fluctuation has been an effective ecologic force causing the development of a woolgrass marsh in a habitat where a cattail marsh would be expected.

One of the most interesting aspects of this woolgrass marsh is the fact that the species associated with the woolgrass are still essentially the same as one would expect to find with cattail. Apparently the water level fluctuation has been much less effective in altering the structure or composition of the community than in respect to the physiognomic dominants themselves.

This then raises the question of the role of woolgrass or cattail in this community. If little or no change occurs in the associated species when one is replaced by the other, either they are almost exact ecologic equivalents, or their role in this community is dominant in physiognomy only. This latter alternative is somewhat difficult to accept in view of the density and vigor of growth and the degree of shading of both cattail and woolgrass stands. It seems more likely that a high degree of ecologic equivalence in this situation is involved, with dominance perhaps determined by the pattern of water level fluctuation. The occurrence of woolgrass in large marshes with no water level control indicates this is not the sole factor involved, however. A study of the full range of woolgrass communities would no doubt indicate that it is ecologically distinct from cattail in many cases. It is quite possible that the particular situation discussed here merely represents a point of overlap in the ecology of woolgrass and cattail.

SUMMARY

A woolgrass (*Scirpus cyperinus* (L.) Kunth) community in Juneau County, Wisconsin was studied by means of belt transects in August, 1951. Species composition and cover values for a total of 35 stand samples were recorded.

Units based on a field technique of recording data by samples of physiognomic homogeneity revealed a very definite structure. These types were distinguished: woolgrass-grass, woolgrass-spikerush, and woolgrass-sedge. Analysis showed these types to be related to water depths and allowed development of a hypothesis of the successional trends of these units.

The dominance of woolgrass in a community similar in almost all respects to cattail communities was probably due to the pattern of water level fluctuation. The results of this study indicate a close ecologic relationship between cattail and woolgrass.

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MICROBIOLOGICAL STUDIES OF ARCTIC SOILS[1]

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Reports from several laboratories have confirmed the presence of microorganisms in arctic soils. Kazansky (1932) found a variety of groups of bacteria in seven soil types examined at Novaya Zemlya and observed bacteria in all horizons of three of the soils. The presence in soils of the Soviet Arctic of several groups of bacteria which were common to temperate areas was reported by Issatschenko and Simakova (1934) who thought these isolates to be specific strains which were selectively developed under conditions of low temperature. Quantitative studies were carried out by Levinskaya and Mamivcheva (1936) on peat and sand-clay soils at Murmansk on a year-round basis. The bacterial population was lower than normally found in temperate zones, and the highest counts were observed during the winter months and to a lesser extent during autumn. Paradoxically, Egorova (1938) isolated thermophilic bacteria from soils of islands in the Kara Sea, and McBee and McBee (1956) reported that, in some cases, thermophiles are present in soils of the Point Barrow area of Alaska, especially near old Eskimo dwellings.

The present study is concerned with the seasonal changes which take place in the bacterial flora of arctic soils and presents data which show that the soil population is active for a short time during the summer months in carrying out transformations necessary in the maintenance of soil fertility.

METHODS

Three different areas were selected for study and were marked with a quadrat 15 feet square. The first site (Fig. 1) was located behind a fresh water lake in an area of high center polygons consisting of peaty soil covered with lichens and other arctic plants. The area sampled was high enough to afford good drainage during the summer thaw. A beach ridge not far from the first location was selected for the second area of study. The predominant soil type of this area was the arctic brown soil described by Tedrow and Hill (1955), and all samples studied consisted of a sandy-loam soil. The third site, situated on a bluff overlooking a salt water lagoon, was made up of a sandy-loam interspersed with areas of peat and afforded a soil type intermediate in composition to the other two soil types.

Three soil samples were collected from the A horizon (7 to 12 cm below surface) of each station approximately every 10 days. Physical measurements such as air temperature, soil temperature, and snow cover were also made at the time of sampling. Soil moisture was determined by drying a 10 gm sample at 110°C to constant weight; soil pH was determined on the dried

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[1] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and the Arctic Institute of North America. Reproduction in whole or in part is permitted for any purpose of the United States Government.

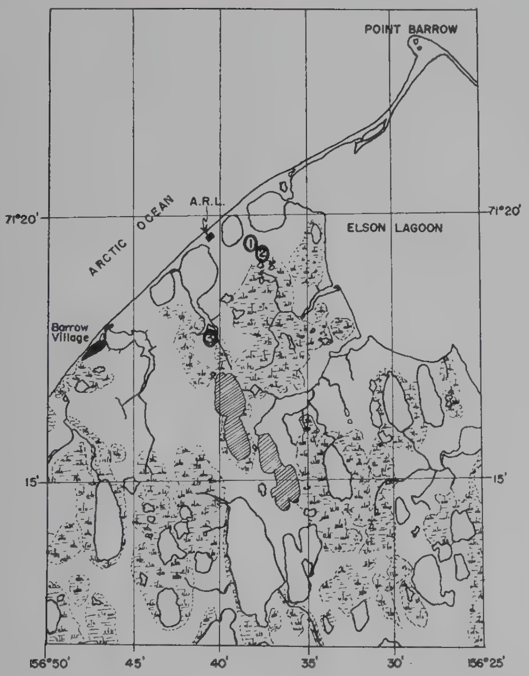

FIG. 1. Sketch-map of Point Barrow region showing the areas sampled.

samples using a Hellige-Truog field soil testing kit.

A dilution series was prepared from an original 10 gm sample of each soil, and 5 plates for each of the different media were poured from selected dilutions. Prior to counting, incubation was carried out for 5 days at 22°C for plates poured with nutrient agar (Difco), Sabouraud's dextrose agar (Difco), and Thornton's standardized medium (Allen, 1951). An additional series of nutrient agar plates was also incubated at 2°C for 14 days. The number of thermophilic bacteria was ascertained by incubating dilutions prepared with nutrient agar and nutrient agar plus 0.5 per cent glucose at 55°C for 48 hours. A running average of bacteriological counts and all other data collected from two successive sampling periods was used in determining the points plotted in Figs. 2, 3, and 4.

Qualitative and quantitative activity experiments were carried out using techniques outlined by Allen (1951).

RESULTS

Counts of bacterial colonies on nutrient agar plates are plotted in Figs. 2, 3, and 4. In most cases the highest counts occurred in spring (April-May) with lesser highs observed in late winter for plates incubated at 22°C. Although the numbers were slightly lower, similar trends were observed when Thornton's standardized medium was used. These data confirm the observations of Conn (1914) who, when working in a temperate climate, found the highest counts of bacteria in soils in February and a drop in numbers as the thaw occurred. A sharp drop in numbers of bacteria was observed also in the arctic soils studied following the summer thaw. Conn attributed the high to actual growth and stated that both a summer and winter flora exist. From the soil temperatures reported in Figs. 2, 3, and 4, it hardly seems likely that bacteria could reproduce under these extreme conditions. The apparent rise in population would appear to be the result of some physical phenomena such as the breaking up of clumps of bacteria brought about by the freezing of the soil.

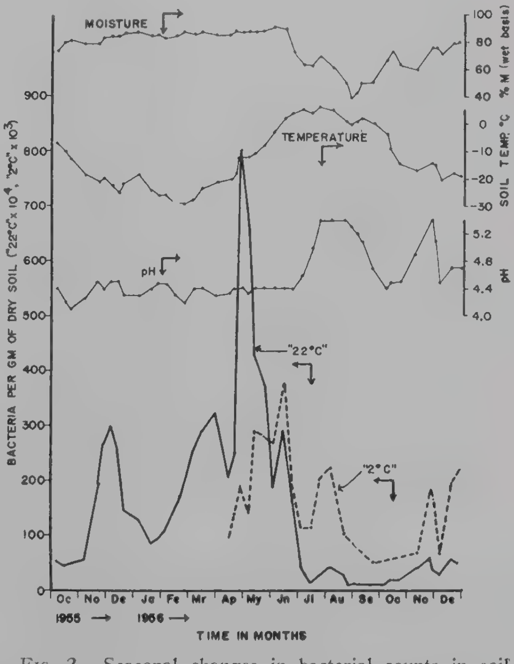

FIG. 2. Seasonal changes in bacterial counts in soil samples collected at area no. 1. The "22°C" x 10^4 represents the count x 10^4 obtained for plates incubated at 22°C, the "2°C" x 10^3 represents the count x 10^3 obtained for plates incubated at 2°C.

Since the maximum summer soil temperatures for the three areas studied ranged between 8°C and 11°C (7 cm below surface), it is quite possible that during the summer and late fall the increase in counts of samples cultured at 2°C represents true multiplication and that it is this group which is responsible for chemical transformations taking

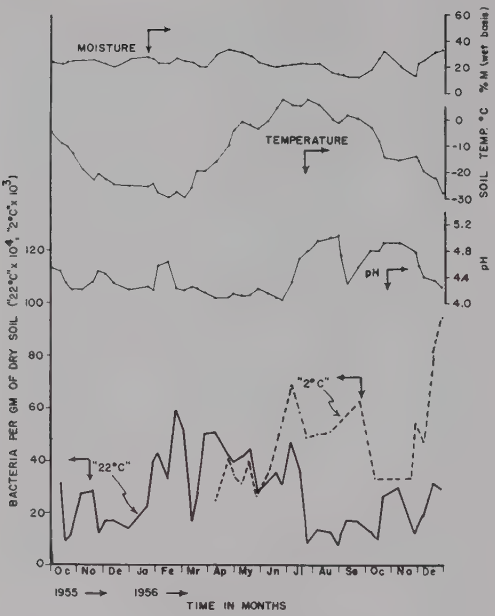

FIG. 3. Seasonal changes in bacterial counts in soil samples collected at area no. 2. Legend as for Figure 2.

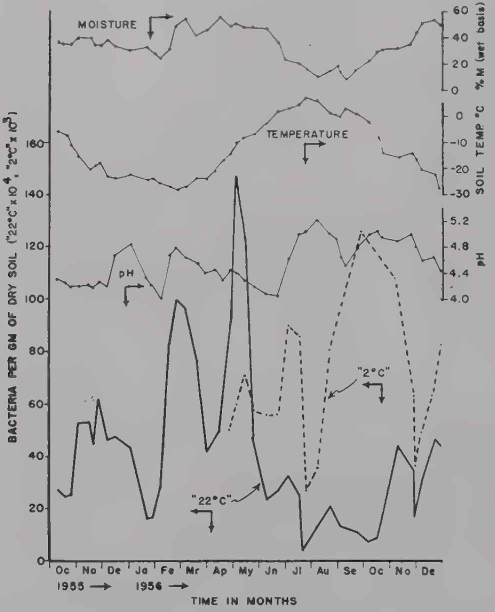

FIG. 4. Seasonal changes in bacterial counts in soil samples collected at area no. 3. Legend as for Figure 2.

place in the soil which result in soil fertility. No data are available to date to show if this group is composed of psychrophilic or, for the most part, mesophilic groups growing at a slower rate at reduced growth temperatures.

Thermophilic bacteria

Thermophiles were isolated occasionally from all three sites as well as from samples of beach gravel studied during the winter of 1954-55, thus confirming the observations of Egorova (1938) and McBee and McBee (1956). However, in most cases the number of thermophilic bacteria was so low as to be insignificant in all of the soils studied. Counts were aproximately the same on both of the media used. The role played by this group of microorganisms in the economy of arctic soils still remains obscure.

Comparative studies of soils of other areas

During the month of August 1956, it was possible to fly to 5 other coastal areas of northern Alaska between Point Lay and Barter Island. At each location, 3 samples each of 2 different soil types were obtained and analyzed upon returning to Point Barrow. In all cases, cultures were prepared no later than 5 hours after the samples had been collected. Average counts of the 3 samples of each soil are given in Table I. Counts of fungi on Sabouraud's dextrose agar ranged from 600 to 7,000 per gram of dry soil but were not necessarily highest in those samples having the more acid soil pH as might be expected. Although significant numbers were observed in all cases, the population, in general was lower than ordinarily encountered in soils of warmer regions.

In some cases, the counts obtained on nutrient agar and Thornton's agar were in the same range of magnitude, which was also true for all soils of the year-round studies at Barrow. Although the greatest number of bacteria in both media was observed from peat soil from Pitt Point, the highest count for plates incubated at 2°C was observed from a peat soil from Point Lay. These data suggest that the portion of the total population which can be cultivated at low temperature will vary and is not necessarily a function of the number which will grow at 22°C. Moreover, in all cases, soil pH, soil moisture, soil temperature, and air temperature did not appear to be the sole factors in determining the total microbial population which could be cultivated under these conditions.

Since each area was sampled on only one occasion, the amount of precipitation, temperature ranges, etc., were not known. However, with the exception of the Pitt Point samples, counts were higher in more southernly latitudes.

TABLE I. Microbiological studies of soils of the Arctic Coast of Alaska

Area	Point Lay		Wainwright		Barrow		Cape Simpson		Pitt Point		Barter Island	
Date	8-21-56		8-21-56		8-27-56		8-7-56		8-7-56		8-31-56	
Soil type	peat	loam	peat	sandy loam	peat	sandy loam	peat	sandy loam	peat	clay	loam	loam
Air temp. (°C)	2	2	0	0	0	−1	6	6	5	5	3	3
Soil temp. (°C)	3	3	2	2	0	−1	5	4	5	7	1	1
Soil pH	6.0	6.1	5.0	5.4	5.4	4.9	6.0	5.5	6.0	7.2	6.5	6.4
Moisture (%)	43.9	12.7	51.6	8.9	50.1	12.1	60.7	20.0	66.6	33.0	7.8	21.7
Bacteria[1] (nutrient agar)												
[2]“2 ° C” x 10^4	51	30	38	4	10	7	14	5	17	9	13	25
[3]“22° C” x 10^4	97	61	86	7	17	9	24	33	130	49	15	29
[4]“55° C” x 10^1	0	0	0	0	0	0	2	1	8	11	0	0
[3]“22° C” x 10^4(Thornton's agar)	100	67	102	10	25	8	19	27	156	49	17	29
Fungi[1] (Sabouraud's agar)												
[5]“22° C” x 10^2	14	14	45	6	28	14	70	17	54	14	15	25

[1] Per gram of dry soil. [2] Incubated at 2° C, counts x 10^4. [3] Incubated at 22° C, counts x 10^4. [4] Incubated at 55° C, counts x 10^1. [5] Incubated at 22° C, counts x 10^2.

Studies of the nitrogen cycle

A series of media containing various nitrogen sources was inoculated with soil from all three study plots in the Barrow area and incubated at 2°C, 22°C, and under tundra conditions (1°C to 11°C). These media included: (1) Stephenson's medium containing either ammonium sulfate or sodium nitrite for the detection of autotrophic nitrifying bacteria; (2) potassium nitrate-glucose broth for demonstrating denitrification; and (3) casein-glucose medium and urea-beef extract medium for the determination of ammonification by heterotrophic microorganisms. Special care was taken to cover the caps of those bottles imbedded in the tundra soil with paper and then with a layer of soil in order to insure true tundra incubation temperatures. At the end of 6 weeks (6-28-56 to 8-9-56) samples were removed and tested for the presence of nitrate, nitrite, ammonia, and pH changes; aliquots from the casein and urea media were titrated with N/50 sulfuric acid using methyl red indicator. On August 10, a second series of media was prepared and run concurrently with the former series until September 10 when all were removed for final testing.

No autotrophic nitrifiers were found to be present in any of the soils. Microorganisms capable of carrying out nitrate reduction ($NO_3^- \rightarrow NO_2^-$) were present in all soils incubated under tundra conditions, but no denitrification took place.

The results of quantitative ammonification-in-solution studies are given in Table II. Although the results of these experiments are variable, some activity was observed in all cases when the media were incubated under tundra conditions. Similar results for the casein medium were obtained for the second series incubated from August 10 to September 10. Several of the bottles of urea medium were disturbed by foxes which were very prevalent at this time, and these data were not considered valid. Although these studies are preliminary in nature, they strongly suggest that the microbial flora is active during the summer months.

DISCUSSION

Arctic soils can support relatively large numbers of bacteria and when cultural techniques are employed, in some cases approach the counts (generally 2 to 60 million per gram of soil) for temperate soils (Waksman 1946). In many cases, the counts at 22°C obtained on soils of the Alaskan Arctic were greater per gram of either wet or dry soil than those reported by Levinskaya and Mamivcheva (1936), who obtained maximum soil counts of 100,000 to 157,000 bacteria per gram of a sand-clay soil at Murmansk. Thermophilic bacteria were found occasionally in most of the soils studied, but their numbers were so insignificant that their role in soil fertility is probably of little or no significance.

Soil temperatures along the Arctic Coast are below freezing for most of the year (9 to 10 months), and during the summer of 1956 reached a maximum of +11°C. It is highly improbable that any growth or microbiological activity occurs during winter months when soil temperatures remain well below 0°C, although an apparent rise in population is observed during the prolonged period of freezing with a significant drop in numbers once the thaw occurs.

A portion of the population can grow at reduced temperatures (2°C) when the incubation is lengthened from 5 days to 14 days. This group shows an increase in numbers during the summer months and is probably responsible for any chem-

TABLE II. Ammonia-nitrogen production of arctic soils

		CASEIN SOLUTION			UREA SOLUTION		
Sample	Incubation conditions[2]	Dry wt. (gm) of inocula per 100 ml medium	Final pH	Mgm NH_3-N produced per 100 ml medium[1]	Dry wt. (gm) of inocula per 100 ml medium	Final pH	Mgm NH_3-N produced per 100 ml medium[1]
Control	22° C	None	7.1	4.85	None	8.6	200
Sandy-loam[3]	2° C	0.387	6.3	0.00	0.387	9.3	326
(area No. 2)	22° C	0.387	6.4	11.80	0.387	9.3	157
	Tundra	0.387	6.3	0.03	0.387	9.3	545
Peaty-loam[4]	2° C	0.039	6.1	0.00	0.392	9.3	545
(area No. 3)	22° C	0.039	8.5	23.45	0.392	9.3	518
	Tundra	0.039	7.1	6.65	0.392	9.3	317
Peat[5]	2° C	0.023	7.1	7.75	0.077	9.3	314
(area No. 1)	22° C	0.023	8.8	12.65	0.077	9.4	550
	Tundra	0.023	9.6	4.70	0.077	9.3	73

[1] Control values have been subtracted from all experimental values. [2] Six weeks incubation, 6-28-56 to 8-9-56. [3] 22.6 per cent moisture; pH of soil, 4.0. [4] 21.6 per cent moistrue; pH of soil,4.1. [5] 84.7 per cent moisture; pH of soil, 4.3.

ical transformation taking place. Brower (1942) reported that the Eskimos of the Barrow area buried bearded seal skins in the soil during the summer prior to the construction of oomiaks (skin-boats) in order that they would be rotted to the point that the hair could easily be removed. Indirectly, this practice strongly suggests the presence of an active soil microflora. Moreover, the results of quantitative and qualitative experiments, although preliminary in nature, suggest also that limited microbial activity does take place during summer.

SUMMARY

A study of microorganisms of arctic soils was carried out from October 1955 through December 1956. The highest counts for plates incubated at 22°C were observed when the soil was frozen, and a sharp drop in numbers was observed once the summer thaw had occurred. A portion of the population was capable of growth at 2°C and increased in numbers during the summer and early fall when the soil temperature was above freezing. Preliminary qualitative and quantitative soil activity experiments were carried out which strongly suggest that limited microbial activity takes place in the soil during the summer.

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PRODUCTION OF HERBACEOUS VEGETATION IN OPENINGS AND UNDER CANOPIES OF WESTERN ASPEN

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Extensive forests of quaking aspen (*Populus tremuloides* Michx.), which occur widely at intermediate elevations in the Intermountain and Rocky Mountain West, constitute an important resource, both esthetically and economically. The aspen type is esteemed among sightseers, picnickers, and campers because of its beauty. Aspen forests protect the soil of an important snow-collecting belt on western mountain watersheds. Although aspen is not one of the important timber species, aspen wood products are in considerable and increasing demand. Finally, the type supports undergrowth capable of furnishing a great amount of cover and forage for wildlife and livestock. On aspen range in good condition one may wade waist deep through a rich mixture of many plants, including species of Heracleum, Mertensia, Delphinium, Osmorphiza, Agastache, Erigeron, Rudbeckia, Senecio, Thalictrum, Agropyron, Bromus, Elymus, and Carex. Most aspen range in the Intermountain region is depleted from prolonged overgrazing, however, and palatable species that were formerly abundant are likely to be scarce or absent.

Curiously, much less vegetation is produced in openings, as a rule, than beneath the aspen canopy.[3] Usually the vegetation of openings is the sparser and shorter, and it tends to include a smaller proportion of desirable forage species (Houston 1954). It may, indeed, include undesirable species such as the annual *Madia glomerata* Hook., that are absent under the aspens. We have personally observed such differences in production and species composition on aspen ranges in Utah, Nevada, southern Idaho, western Wyoming, and western Colorado. These observations have included a great variety of sites with respect to soil and exposure, and many variations in character of vegetation.

Why should such a difference in ground-cover production exist? Is it a product of those factors responsible initially for the existence of openings in an aspen forest? Is it caused by differences in microclimate under and away from the aspen canopy? Is it a result of heavier grazing in openings than under the aspen? Or is it the result of interactions between some or all of these factors?

Whatever the cause, this widely observed difference seems anomalous, because it would appear that demands upon the environment by the aspen trees themselves might be expected to infringe on the needs of plants of the shrub and herb layers. Logically, therefore, being free of such competition, the openings should produce more vegetation, not less, than equal areas under aspens. Such a relation has been described by Moinat (1956) in the *Quercus gambelii* type in southwestern Colorado, a zone somewhat warmer and drier than the aspen-fir zone. Moinat shows that production of the field layer in grassy parks is markedly higher than in scrub-oak thickets.

Many trenching experiments (reviewed by Korstian and Coile 1938) have demonstrated the adverse effects of root competition by forest overstory on growth of native ground vegetation or artificially planted trees. Shirley (1945), in a study carefully designed to test the relative effects of shade and root competition of aspen and jack pine on tree seedlings and planting stock in Minnesota, demonstrated a root-competitive depression of conifer growth, although not of survival. Shirley's comment is that, "In these studies, however intense the root competition of the overwood, its effect on survival was more than offset by the benefits of the shade, provided this did not reduce the light intensity below 20 percent." We know of no experiments of this kind involving western aspen except for Pearson's (1914) comparisons of survival of planted Douglas-fir under aspen and in openings. These showed better survival under aspen.

Methods

The present study was designed to measure the productivity of herbaceous vegetation beneath aspen canopies and in adjacent openings where basic site factors appeared to be the same. Grazing by livestock was excluded, but deer had access to three of the four study sites, and rodents and rabbits to all four. The study areas were spaded up and seeded artificially so that the same species could be compared. In order to evaluate the competitive effects of aspen roots, additional plots under the aspen trees were trenched.

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[3] The herbaceous vegetation in a narrow zone within the edges of some aspen stands, where livestock "shade up," may be more severely depleted than vegetation in the open, but this is not true under aspen canopy generally.

The study was begun in the fall of 1950 at four sites ranging in elevation from 8,050 to 9,000 feet in Ephraim Canyon in central Utah. These four sites pretty well bracket the continuous aspen type in Ephraim Canyon, although isolated patches of aspen occur both at lower and higher elevations. Nine plots, each 10 feet square, were laid out at each site. Six plots were placed under the aspen canopy in pairs, and three were placed in opening 25 to 75 feet away from the aspen edge. The plots under aspens were so placed as to avoid unnecessary removal of trees.

One member of each pair of plots under aspens was trenched in the fall of 1950 to a depth of about 18 inches to cut the aspen roots. This treatment also cut any roots of the shrubby and herbaceous undergrowth that might have extended into the trenched plots. The trenches were then refilled with soil. Trenching, followed by refilling, was done each year during the course of the study.

Each plot was divided into four subplots 5 feet square, and each subplot was seeded to a different species, using seed collected in Ephraim Canyon. Four native species were used: *Bromus carinatus* Hook. & Arn., *Elymus glaucus* Buckl., *Rudbeckia occidentalis* Nutt., and *Heracleum lanatum* Michx.

Each subplot was planted with five rows 5 feet long and 1 foot apart. All data were taken from the inner three rows, ignoring 0.9 foot at each end and the outer two rows to avoid border effect. This left 9.6 square feet as the area of each subplot.

Seeding was done in the fall of 1950 at a rate of about two seeds per inch of row. In the spring of 1951, all stands were thinned to one plant per 2 inches of row, and that fall bare spots were reseeded. The plantings were weeded periodically.

Considerable difficulty was experienced in getting stands on all plots, particularly the open plots. Full stands were important to success of the comparison, since we were concerned with measurement of differences in productivity rather than differences in success of germination or of seedling establishment. Because full stands were not achieved uniformly, the plantings were rated in 1952 and 1953 on a scale from 0 to 5 as to abundance and distribution of plants. In the comparisons that will be made, only the better stands, classes 3, 4, and 5, will be used—except in those instances where a poor stand outproduced a stand having a higher rating.

In the fall of 1951, the grasses Bromus and Elymus were harvested at a height of 1 inch, and their weights were used as part of the data for a preliminary report (Houston 1952). The clipping treatment did not appear to hurt Bromus, but it seems likely that some plants of Elymus were killed and the stands thereby reduced. In the fall of 1952 the weight of all species was estimated (Pechanec and Pickford 1937). In September 1953 all plants were harvested to ground level. The herbage was taken into the laboratory in paper sacks and brought to air-dry weight. These weights, expressed in grams per 9.6 sq. ft. (or, multiplied by 10, in pounds per acre), form the basic data used in this report. They consist of three components: (a) the species planted, (b) weeds persisting in spite of cultivation, and (c) estimates for losses from current utilization by deer and rabbits. For most harvests, components (b) and (c) were not large, but including them gives a closer approximation to true production than would be possible if they had been omitted.

Total precipitation during the growing seasons of 1951 and 1952 was slightly above average, and in 1953 it was materially greater than average (Table 1). September precipitation was below average in all 3 years, but precipitation so late in summer, when most herbage has dried adds little to plant growth. The spring of 1953 was very late. Because of a late storm, snow did not leave the open plots at the lowest area until May 14 and at the highest area until June 6. Scantiness of precipitation during June was therefore not so harmful to plant growth as it might be in some years. Precipitation was well distributed during July and August. It seems probable, therefore, that the 1953 season, the year of harvest, was an especially good one for plant growth.

Temperature records show nothing distinctive about the three growing seasons except that min-

TABLE 1. Monthly precipitation in inches at Headquarters during the three growing seasons of this study, 1951 to 1953, in comparison with the average

	Average 1934-48 incl.	1951	1952	1953
May	2.02	2.85	3.00	4.27
June	1.82	1.27	2.69	0.34
July	1.57	1.41	1.14	4.83
August	1.50	2.81	1.08	1.12
September	1.24	0.21	0.48	0.13
Seasonal	8.15	8.55	8.39	10.69

ima tended to be lower than average in both 1951 and 1953.

Climatic observations were not made at the individual study areas. From long-time records in Ephraim Canyon it may be estimated that average daily temperatures are about 3.5° F. lower at the highest station than at the lowest (Price and Evans 1937). Average annual precipitation may be estimated to vary from about 23 inches at the lowest station to 27½ inches at the highest, and growing-season precipitation, May through September, from about 7 to 8 inches (Lull and Ellison 1950). These values have been computed from relations determined over a much greater elevational range; between our four sites they may be modified materially by local topographic factors. For example, the highest site with a westerly exposure and the next highest with a southerly exposure may well be warmer than the two lower sites with near-level northerly exposures.

RESULTS

Table II shows that production of *Bromus carinatus* on the untrenched plots under aspen was materially less than on either the trenched plots under aspen or on the open plots. Both differences, which are statistically significant ($P < .01$), are illustrated in Figures 1 and 2. From these differences it would appear that the natural potential for production of Bromus in aspen openings is greater than under an aspen canopy, and that aspen root competition—together with root competition of surrounding shrubs and herbs—is important in depressing yields of undergrowth.

TABLE II. Air-dry production of *Bromus carinatus*, in grams per 9.6 square feet, at four sites in Ephraim Canyon, 1953

	Under Aspen		
Site and elevation	Trenched	Untrenched	Open
Bluebell (9,000 ft.)	171	30*	128
Headquarters (8,800 ft.)	133	58	116
Snowberry (8,450 ft.)	97	17	47
Aspen (8,050 ft.)	89	36	51
Weighted average	122.5	35.9	85.5

*Average from 2 subplots only. See Table III and text.

In 1951 yields were about one-fifth of those in 1953, averaging 22.9, 5.3, and 21.7 grams for the trenched, untrenched, and open treatments respectively. Estimated yields in 1952 tended to be intermediate between yields of 1951 and 1953. The question may well be asked, therefore, whether maximum production had been achieved in the third year. Possibly it had not; but it is also unlikely that production would have increased greatly in subsequent years because much of the rise in production the third year can be attributed to an unusually favorable growing season.

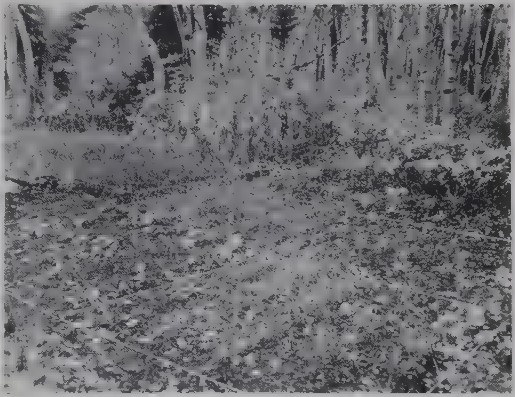

FIG. 1. Untrenched (foreground) and trenched plots at Snowberry Sept. 26, 1953, just before harvest. The trenched plantings show marked release from overstory root competition. Nearest untrenched subplot was planted to Bromus, subplot to left of it to Rudbeckia, to right of it to Heracleum, and directly behind it to Elymus. Adjacent trenched subplot was also planted at Elymus, to left of it to Bromus, to right of it to Rudbeckia, and directly behind it, with some of the large leaves barely visible through the grass, to Heracleum. Upright frame is 1 meter square.

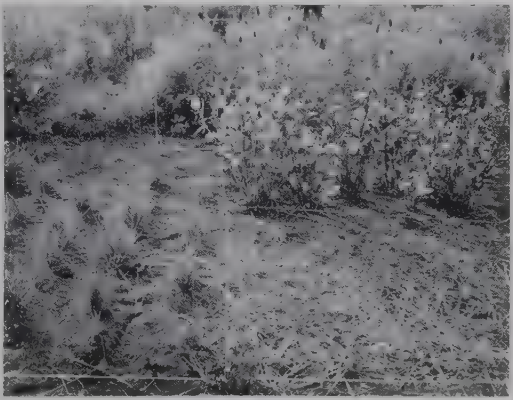

FIG. 2. An open (untrenched) plot at Snowberry, Sept. 26, 1953, just before harvest. Bromus is in left foreground, Rudbeckia in right background. On this plot the stand Elymus (left background) is very poor, and no stand of Heracleum (right foreground) has been obtained, despite use of a straw mulch upon a repeat seeding. Upright frame is 1 meter square.

In 1953 plants on the trenched plots were markedly taller (88 cm) than plants on the untrenched plots (68 cm); and the latter were about the same height as the much heavier plants on the open plots (67 cm).

There is also a suggestion in Table II of increasing production with increasing altitude.

Open yields ($r = .82$, $P < .01$) and trenched yields ($r = .62$, $.05 > P > .01$) are significantly correlated with altitude, but untrenched yields are not. Thus, whatever the favorable factors that increase with altitude in this study (probably precipitation and insolation), it appears that aspen root competition masks their influence on the ground cover. Perhaps this means that the aspen is dominant over other vegetation in a physiological as well as a physiognomic sense.

One of the untrenched plots at Bluebell gave materially higher yields than the others (Table III). This yield of 189 grams is more than twice as great as that on any of the other 11 untrenched plots of Bromus in this study, and is of the order of the yields from the trenched plots. Yields of other species on this plot were also exceptionally high in 1953; estimated yields of all species were markedly higher on this plot than on the others in 1952; and the clipped yields of Bromus and Elymus in the seedling year 1951 were also higher on this plot than on the others. Although this aberration was puzzling at first, an examination of the overstory aspen in 1953 provided the explanation: most of the trees surrounding this particular plot had died! In 1955 only 6 living trees 1 inch DBH and over were within 10 feet of the edges of this plot, whereas there were 17 trees within the same distance from each of the other two untrenched Bluebell plots. Essentially, then, the plot may be considered to have been freed from aspen competition about as effectively as if it had been trenched. For this reason, the data from this plot are excluded from Table II and from corresponding tables for the other three species. The plot does have value, however, if the foregoing explanation is valid, in corroborating the effects of trenching.

TABLE III. Air-dry production of *Bromus carinatus* at Bluebell, in grams per 9.6 square feet, 1953

	UNDER ASPEN		
	Trenched	Untrenched	Open
	117	26	157
	230	34	124
	167	189	104
Average	171.3	83.0	128.3

Yields of *Elymus glaucus* (Table IV) show the same essential relations as those of Bromus. Production on the trenched plots greatly exceeds production on the untrenched plots under aspen ($P < .01$). Average production in the open is greater than on the untrenched plots under aspen at the two upper sites, but the difference is not statistically significant. Nevertheless, taking into account the fact that all the open plots are not fully stocked, it seems probable that the potential for production of Elymus is greater in the open than under aspen. Open stands that had been rated fair to good at Snowberry in 1952, and that had been rated poor to fair at Aspen, had too few plants left by the fall of 1953 to warrant harvesting.

TABLE IV. Air-dry production of *Elymus glaucus*, in grams per 9.6 square feet, at four sites in Ephraim Canyon, 1953

	UNDER ASPEN		
Site and elevation	Trenched	Untrenched	Open
Bluebell (9,000 ft.)	264	75*	124†
Headquarters (8,800 ft.)	110	34	57†
Snowberry (8,450 ft.)	84	14	.....
Aspen (8,050 ft.)	109	50	.....
Weighted average	141.7	40.1	90.5

*Average from two subplots only. †Some subplots not fully stocked.

In 1951 yields of Elymus on the trenched aspen and open plots were the same, 27.8 grams; on the untrenched plots under the aspen they were only 5.7 grams. Estimated yields in 1952, as with Bromus, were intermediate between yields of 1951 and 1953.

In 1953 at Bluebell and Headquarters, Elymus plants on the trenched plots were tallest (102 cm) and on the open plots shortest (81 cm). Plants on the untrenched plots were intermediate in height (87 cm). This, taken together with their light weight, reflects the characteristic spindliness of untrenched plants.

A suggestion of increasing Elymus production with increasing altitude exists in Table IV. Trenched yields are correlated significantly with altitude ($r = .59$, $.05 > P > .01$). Too few outside yields are available, with the variation that exists, to give a significant correlation. Untrenched yields, as with Bromus, show no correlation with altitude, suggesting again that aspen root competition obscures the relation.

Yields of *Rudbeckia occidentalis* in the open average a little higher than those on the trenched plots under aspen (Table V); both are significantly greater ($P < .01$) than yields on the untrenched aspen plots. If the open plots had been fully stocked, it seems probable that they would have materially outproduced the trenched plots under aspen. Estimated yields in 1952, which were somewhat lower, tended to show the same relations.

Production on the trenched and open plots in

TABLE V. Air-dry production of *Rudbeckia occidentalis*, in grams per 9.6 square feet, at four sites in Ephraim Canyon, 1953

Site and elevation	Under Aspen		
	Trenched	Untrenched	Open
Bluebell (9,000 ft.)	288*	42*	.....
Headquarters (8,800 ft.)	130	44	236
Snowberry (8,450 ft.)	186	8	186†
Aspen (8,050 ft.)	156	86*	214*†
Weighted average	180.8	41.3	211.4

*Average from 2 subplots only. †Some subplots not fully stocked.

TABLE VI. Air-dry production of *Heracleum lanatum*, in grams per 9.6 square feet, at four sites in Ephraim Canyon, 1953

Site and elevation	Under Aspen		
	Trenched	Untrenched	Open
Bluebell (9,000 ft.)	60	4*†	...
Headquarters (8,800 ft.)	23*	5*†	.
Snowberry (8,450 ft.)	42	3†	.
Aspen (8,050 ft.)	20*†	4*†	
Weighted average	39.2	3.7	

*Average from 2 subplots only. †Subplots not fully stocked.

1953 shows a slight positive correlation with altitude, but neither is statistically significant.

The average of 86 grams for two untrenched subplots at Aspen is probably unduly high. One of the subplots was flooded by runoff from a road and produced 145 grams, more than five times as much as the other.

Two bits of evidence indicate that the blank in Table V, and probably the poor stocking of the open plots at the two lower stations, were due to difficulty in initial establishment, rather than to unfavorable growing conditions for established plants. First, the three Rudbeckia plants growing on the three open plots at Bluebell in the fall of 1953 were very robust. The same can be said for plants on the understocked plots at Snowberry and Aspen. Second, Rudbeckia grows naturally and abundantly in openings throughout the aspen zone, and particularly at Bluebell.

Much of the differences in weight between treatments in 1953 is created by differences in numbers of Rudbeckia flower stems. Plants on the untrenched aspen plots produced few stems, and a high proportion of these produced no flower heads. These plants averaged only 55 cm in height. The taller, more robust plants on the trenched aspen plots (82 cm) and on the open plots (81 cm) produced abundant, heavy stalks bearing a high proportion of heads.

Yields of *Heracleum lanatum* are 10 times as high on the trenched plots under the aspen as on the untrenched plots (Table VI). The difference is significant statistically ($P < .01$), and is compounded of two factors, a difference in size of plants, and a difference in stocking. Heracleum plants were over twice as tall on the trenched plots (13 cm) as on the untrenched plots (6 cm), and they were almost twice as numerous—59 per plot as compared with 33.

None of the untrenched plots had fully stocked stands, and it therefore appears that the competitive effect of aspen was marked not only in terms of plant size, but in a material difference in successful seedling establishment. This effect of aspen on stand establishment is also reflected by the other species, but by none so sensitively as by Heracleum.

In 1952 estimated yields, although lower than 1953 yields, showed the same essential difference between treatments as in 1953.

The trenched plots show a positive correlation between altitude and production, but this is not significant statistically. A positive correlation between altitude and abundance of plants per plot is significant, however ($r = .81$, $P < .01$). The corresponding correlations for the untrenched plots are much weaker, as has been noted with production of other species.

No full stands of Heracleum were produced on the open plots, and most open plots had no plants of Heracleum at all in the fall of 1953. The plants that were present in 1953, however (on two plots at Bluebell and two plots at Headquarters), were thriving and large. Their robust growth was doubtless partly a result of reduced competition, for these few plants had the cultivated area of their subplots to themselves; but it also indicated that the limiting factor in these plantings of Heracleum—at the two uppermost sites, at least—was connected more with difficulty in seedling establishment than with the species' inability to grow in the open.

Observations Since 1953

The plots have been observed during the 3 years since 1953, although trenching and weeding have been discontinued. The differences noted from 1951 to 1953 have persisted through 1956. On the open plots in 1956 Bromus and Rudbeckia were vigorous, but most of the Elymus had disappeared. The differences in vigor of plants on the trenched and untrenched plots under the aspen were still visible (Fig. 3). A rough attempt was made in July 1956 to compare the volume of herbage produced on the trenched and untrenched plots with that produced by the undisturbed un-

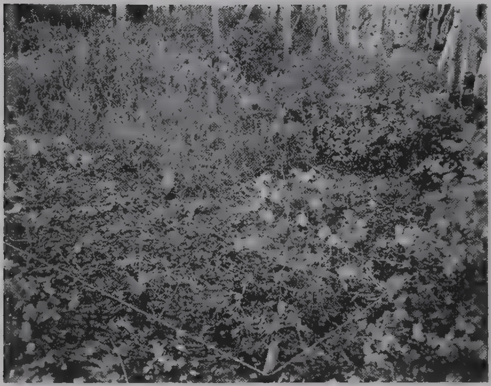

FIG. 3. The same two plots as in Fig. 1, on Aug. 26, 1956. Even 3 years after trenching there is markedly greater growth on the trenched than on the untrenched plot. Rudbeckia and Heracleum (left and right foreground, respectively) have increased in size since 1953. Upright square-meter frame is between untrenched Elymus to this side and trenched Elymus behind.

dergrowth. The comparison was highly subjective because different species were involved. The open plots did not appear to be producing so great a volume of herbage as the adjacent mixed native vegetation. In general it seemed as if the trenched plots were still producing somewhat more, and the untrenched plots somewhat less, than the undisturbed undergrowth. It seems evident, therefore, that by 1956 the roots of aspen and its undergrowth had not reasserted themselves in the trenched plots, and that the seeded herbaceous vegetation in the untrenched plots, both in the open and under aspen, had not yet built up the vigor possessed by the native vegetation.

The lesson to be learned from these observations is one of caution in applying the results of a short-term study. The seeded vegetation on the untrenched plots is evidently not in equilibrium with the aspen, even 6 years after planting, in the way that the mixed, undisturbed native vegetation is. If the study were to continue for several decades, in other words, presumably the plants on the untrenched plots would be able to secure a greater share of their needs from the soil at the expense of aspen (as undisturbed herbaceous plants presumably do now), and the difference between their production and production of plants in the open would be lessened somewhat. We do not think this difference would cease to exist, however.

DISCUSSION

Insofar as a short-term study can reveal the facts, it seems clear that the potential for production of herbaceous vegetation in aspen openings is greater than that beneath the aspen canopy. It is also clear that a factor limiting production under the aspen is root competition from the aspen trees themselves, or from its undergrowth—or at any rate some factor associated with these roots—since production on the trenched plots was consistently greater than production on the untrenched plots. Except where full stands were not achieved, these patterns were essentially the same for all four species and for all 3 years in which observations were made.

What would competition under aspen be for? The most obvious answer is the soil moisture that trenching releases to the undergrowth. Our only soil-moisture measurements were made at a depth of 3 to 6 inches September 10, 1951, the seedling year. They showed that soil moisture was somewhat higher on the trenched than on the untrenched and open plots (Houston 1952), but it seems unlikely that any such difference would be great with full stands of ground vegetation to utilize the soil moisture. Other studies have also shown soil moisture to be greater on trenched than on untrenched plots (e.g., Fricke 1904, Craib 1929, Korstian and Coile 1938, Shirley 1945).

It is doubtful whether competition for nutrients would be material under the conditions of this study because the fall of aspen leaves, twigs, and gum should return to the soil annually a large part of the nutrients currently being taken up by the trees. It is noteworthy, however, that other trenching experiments (Korstian and Coile 1938, Wallihan 1940) have indicated that soil nitrogen may be slightly greater on trenched than on untrenched plots. This may be a consequence of slightly greater soil moisture.

Shirley's (1945) experiments suggested to him "that factors other than light and soil moisture may be involved in the competition of the undervegetation" with coniferous transplants, and he suggests exudation of toxic substances. Possibly aspen roots inhibit the growth of herbaceous plants by exuding harmful substances or by harboring harmful organisms, but this experiment can throw no light on the question. Some living aspen roots persisted on the trenched plots, as evidenced by sprouts that had to be cut out periodically, but they were probably not numerous enough to balance this influence, if it was an influence, of aspen roots on the untrenched plots.

Unfortunately no trenching was done to evaluate the effects of root competition from woody and herbaceous vegetation surrounding the open plots. These effects may have been material on the open plots since there were shrubs, mainly *Symphoricarpos orephilus,* in the vicinity of most of them.

The poor showing made by Elymus and Heracleum in the open plots may indicate that these species require shade and are unsuited to openings. We think this is unlikely: both species are known to grow well in openings in association with other herbaceous species, although their establishment may be slow. Certainly the failure of Rudbeckia in the open plots at Bluebell cannot be explained in these terms, because it has invaded much comparable overgrazed range. Deficiencies in experimental technique—difficulties in getting seedlings established on the bare, unshaded soil of the open plots—are believed chiefly responsible for the poor stands of these three species.

In light of the fact, established by trenching, that severe competition under aspen reduces herbage production below that of the open, let us return now to the original question: why is the reverse commonly observed, that production under aspen is greater than production in openings?

The most obvious way to explain the differences in production would be to relate them to causes—whatever they may be—of so sharp a contrast in type as that between aspen stands and openings. Unfortunately we do not know why aspen stands and openings exist as they do, so the patterns cannot help in explaining the observed differences in productivity. In many areas it is obvious that aspen is spreading vegetatively into openings, although often the invasion is held in check by browsing of the new shoots by grazing animals. This tendency suggests that the causes of the type boundaries are historical rather than environmental, and that differences in site are not such as to prevent occupance of the openings by aspen. In some areas, however, the aspen edge appears to be static or nearly so, and the hypothesis of a site difference is more tenable. The tendency for invasion is marked at the Bluebell, Headquarters, and Aspen sites of this study, but not at the Snowberry site.

Differences in topography can be ruled out, for commonly there is no change in exposure or degree of slope between an aspen stand and an adjacent opening. Openings seem to occur under all the variations in slope and exposure where aspen forests are found.

No comprehensive comparison of soils under aspens and in adjacent openings has been made, so far as we are aware, and therefore, although the soils in a particular situation appear to be essentially the same, it cannot be stated categorically that this is so. We have observed in central Utah that aspen may be growing on shallow, rocky limestone soils, while deeper soils nearby are dominated by herbaceous vegetation; but this difference is not invariable. There is no clear indication that inherent soil differences are great enough or consistent enough to account for the marked differences that generally exist in the ground vegetation.

The aspen stand itself produces differences in the soil as compared with herbaceous openings. The ground surface under aspen receives a layer of litter from the annual fall of leaves and twigs, as well as litter from the undergrowth, and during the summer there is a constant dripping of aspen gum which eventually finds its way to the soil surface. This litter, together with the canopy itself, protects the soil within aspen stands from erosion. The soil surface of openings, in contrast, receives relatively little aspen litter, and, in consequence of denudation by overgrazing during the past century, many openings have lost considerable topsoil. Thus the obvious differences in soil appear to be more an effect than a cause of the two types of cover.

It is also obvious that microclimate is different in the two habitats. The openings are relatively sunny, warm, and windy; atmospheric humidity is lower, and evaporation near the soil surface is much greater than under the trees (Pearson 1914, Marston 1956). While the soil surface of openings receives more precipitation than the soil surface beneath the tree canopy, because of less interception loss, this difference is probably offset by greater loss of moisture through evaporation. On the other hand, aspens themselves use soil water, and presumably quite a lot, since they are characteristic of fairly moist sites. This use has been measured in northern Utah near the upper limits of the aspen type. The combined water consumption of aspen and its undergrowth there, together with evaporation loss, was estimated to be about 4 inches more per year than evapo-transpiration in nearby herbaceous, perennial vegetation (Croft and Monninger 1953). In that study much of the aspen drain was below the root level of the herbaceous undergrowth, but some of it was no doubt from the upper 4 feet of soil occupied by roots of forbs and grasses.

In short, although herbaceous vegetation may find some advantages in the environment under aspen (greater atmospheric humidity, more fertile topsoil), the advantages of more light and especially more soil moisture in the open appear to outweigh them. But if this be so, should not production under aspen be less, rather than more, than in openings? The experimental results reported here indicate that it should. Except when there was stand failure in the open, and in spite of possible root competition from vegetation surrounding the open plots, production was always higher in the open than on untrenched plots under the aspen.

The differences in production commonly observed are probably a result of differences in grazing pressure. It may be generally observed that livestock, particularly cattle and to some extent sheep, graze in openings more heavily than they graze under aspen. This impression was checked in 1955 by utilization studies on eight sites in and near Ephraim Canyon (Bailey 1956, pp. 75-78). At each site utilization was found to be greater in openings than under the trees, both early and late in the season. While degree of use varied with time of year, plant species, range condition, and class of grazing animal, by fall the utilization was usually two to four times as heavy in the openings as under the aspens. The reason for this difference is probably that the unshaded forage plants in the open manufacture more sugars than plants in the shade of trees, and are therefore relished more by the animals (Welton and Morris 1928, Plice 1951, 1952).

That grazing may be the decisive factor is also suggested by other evidence. First, in stands that have escaped heavy grazing for many years, and that are therefore presumed to be near pristine condition, production in the openings appears to be greater than under the aspen (Houston 1954, Table 2, Area X). Unfortunately such ungrazed areas are few and small, and are mostly in rough, rocky terrain that is not typical of the broad aspen type. Second, the differences in ground vegetation, both in amount and kind, between openings and aspen stands, tend to be greatest where grazing has been heaviest and range condition is poorest. Finally, it may be observed generally that when grazing is reduced on depleted aspen range, desirable plants increase first under the aspens and then spread out into the openings. This has been observed with such grasses as *Bromus carinatus* and *Agropyron trachycaulum* which work out of the aspens to invade openings dominated by *Madia glomerata,* and with such highly palatable forbs as *Osmorhiza occidentalis, Mertensia leonardi, Valeriana occidentalis,* and *Heracleum lanatum.*

It is probable that microclimatic effects associated with severe grazing make difficult the regeneration of moisture-loving species in openings. These effects include the loss of foliage shade from tall herbs (among which are the more moisture-loving, succulent, and palatable species); loss of litter and baring of the soil surface to the full heating and drying effects of sun and wind; loss of soil structure and damage to seedlings because of excessive trampling; and in many places accelerated erosion of the topsoil itself. Because of these effects, shorter, more xeric, less palatable species come to dominate heavily grazed openings. Thus, both directly and indirectly, a difference in severity of grazing appears to be the mechanism by which the contrast in herbage production between openings and under aspen is produced.

That the potential for herbaceous production in openings is greater than under the aspen canopy has at least two important applications in range management:

(a) If the range manager finds production in openings to be as great as or greater than production under the aspens, and particularly if the preferred forage species are about equally abundant, he has reason to believe that the range is producing near its maximum and that it is in good or excellent condition. If production is materially poorer in openings than under the aspen, he has reason to believe that the range is not producing as much as it should, and that it is in fair, poor, or very poor condition, depending primarily upon species composition. In any event, if soil in the openings is bared excessively or shows evidence of accelerated erosion, the range is in unsatisfactory condition (Ellison, Croft, and Bailey 1950). Thus the range manager may use the production of aspen undergrowth as a first approximation to the potential productivity of nearby openings. His estimate may be far from the true productivity if the range has been heavily overgrazed for many years, but he can assume that the openings should be *at least* as productive of herbaceous and shrubby vegetation as the aspen stand.

(b) Because they are the more heavily grazed, the more easily depleted, and the more difficult to restore, openings are the key areas for management of aspen range for livestock. If their productivity and soil stability can be improved or maintained, it is almost certain that the condition of the adjacent range under the aspen canopy will be satisfactory.

SUMMARY

In order to evaluate the potential productivity of aspen openings and the ground vegetation under aspen, plots established in openings and under aspen canopy at four sites were seeded with *Bromus carinatus, Elymus glaucus, Rudbeckia occidentalis,* and *Heracleum lanatum.* Yields at the end of the third season furnish the basis for this report. In order to evaluate the effect of root

competition from aspen, paired sets of plots were trenched to cut the aspen roots.

Plots in the open were much more productive than untrenched plots under aspen, indicating that the potentiality for production in openings is greater than under aspen. (A complication was introduced by the fact that full stands were less consistently attained on the open plots than in aspen shade. This is believed to be a reflection of faulty technique rather than of inherently lower productivity in the open.) The most consistently successful species was Bromus; the least, Heracleum. The results of this study are confirmed by natural areas in which production of herbaceous vegetation in aspen openings appears to be greater than within the aspen stand.

Trenched plots were much more productive than untrenched plots under aspen, which suggests that the principal factor in depressing yields under the aspen is root competition. These effects were still visible 3 years after trenching was discontinued.

A tendency was noted for increased production with increasing altitude. This trend may be related to an estimated increase of 1 inch in summer (May through September) precipitation between the lowest and highest sites, and to warmer exposures at the upper two than at the lower two sites. The trend was noted on the trenched, and to a lesser extent on the open plots, but in no case on the untrenched plots. This suggests that the environmental benefits associated with altitude (e.g., increased precipitation) are more readily taken advantage of by the trees than by their undergrowth.

Utilization of forage by livestock is heavier in openings than under an aspen canopy. Throughout the aspen type this difference in use intensity, together with the more adverse microclimatic effects associated with heavy grazing in openings, is believed to be responsible for the poorer production and species composition commonly noted in openings than under the aspen canopy.

Relative production under aspen canopy and in adjacent openings can be used as an aid in judging range condition. The openings are "key" areas for management.

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THE INITIAL PATTERN OF REVEGETATION OF POCKET GOPHER MOUNDS[1]

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Introduction

The revegetation of the mounds of earth thrown up by the burrowing activities of pocket gophers has received relatively little attention. Weaver and Fitzpatrick (1934) listed *Agrostis hyemalis, Stipa spartea, Aristida oligantha,* and *Euphorbia* spp. as the most common species which grow in the soil of pocket gopher mounds in the tall grass prairie. Bird (1930) mentioned that the mounds of the pocket gopher and earth from badger holes form starting places for *Symphoricarpos* in the aspen parkland area of Canada. Larrison (1942) reported pine seedlings growing in the soil of pocket gopher mounds in the Wenas region of Washington, and Tevis (1956) reported seedlings of red fir becoming established in gopher mounds in a grassland region of California. According to Ellison (1946), gopher diggings provide a relatively unfavorable seedbed in areas where there is little erosion and a good plant cover, but a much more favorable seedbed where much erosion has taken place and the cover has been greatly reduced.

Changes in vegetation due to the burrowing activities of other rodents have likewise received little attention. Ewing (1924) stated that the prairie knolls in northwestern Minnesota, which he describes as "eminences raised by animal agency," are a starting place for shrub species in a normally grassland area. Osborn and Allen (1949) reported concentric zones of vegetation in an abandoned prairie dog town in Oklahoma, from mat forbs in the center, through various stages of secondary succession, to the climax tall grass prairie. King (1955) reported a similar pattern of vegetation in a prairie dog town in South Dakota and attributed the distribution of plants to the differential feeding of the prairie dogs and to the subsoil exposed by their burrowing. Daubenmire (1942) found one plant of *Bromus tectorum* growing in freshly disturbed soil at the entrance to a ground squirrel burrow in the Palouse Prairie region of Washington.

The present study was made during the latter part of the summer of 1952 as part of an ecological study of the pocket gopher (*Thomomys talpoides tenellus* Goldman) in and near the Jackson Hole Wildlife Park near Moran in Teton County, Wyoming. The purpose of the study was to determine what plants first occupy pocket gopher mounds in this area.

Nomenclature of plants and communities follows Reed (1952).

Methods

Gopher mounds were examined in the big sagebrush, streamside forest, and aspen communities in the vicinity of the Wildlife Park. A total of 151 mounds were found to have plants growing in them, 43 in the big sagebrush community, 55 in the streamside forest community, and 53 in the aspen community. The size of the mounds varied from aggregate summer mounds up to 5 feet in diameter to rather small earthen cores 1 to 2 inches in diameter, but most of the mounds were 8 to 16 inches in diameter and 1 to 2 inches thick. Large aggregate summer mounds are formed in some areas when the gophers deposit many loads of earth on the surface at the same point. The gophers burrow in the snow in the winter and later fill some of these snow tunnels with soil. When the snow melts the earthen cores are left on the surface of the ground. Only mounds having plants growing in them were considered but they made up a very small percentage of the total mounds in the communities studied. No attempt was made to determine the exact number of mounds with plants growing in them compared with the number of mounds with no plants growing in them. Each stalk or stem was considered as a single individual for all plants.

The plants growing in the mounds were assigned to 2 categories: (1) plants growing through the mound, i.e., those which had survived being covered by the soil deposited by the gophers and had grown through the mound; and (2) plants growing on the mound, i.e., those which started from seed in the mound. It was sometimes difficult to assign a plant definitely to one category or the other because a plant which has its main roots in the ground below a mound when examined in the fall may have started from a seed in the soil of the mound, or, conversely, some plants which were originally covered by the soil of a mound may have subsequently developed roots in the mound.

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The plants growing through the mounds and on the mounds were further grouped according to the life form classification of Raunkiaer (1934).

Description of Plant Communities

Big sagebrush community

According to Reed (1952) this is the most conspicuous and widespread plant community in the Jackson Hole region. It is dominated by big sagebrush (*Artemisia tridentata*) with an understory of grasses (*Agropyron dasystachyum, Festuca idahoensis, Koeleria cristata, Stipa comata, Bromus* spp., *Poa* spp., and others) and many forbs (*Collomia linearis, Achillea millefolium, Eriogonum* spp., *Lupinus* spp., and others).

Streamside forest community

This community occurs a few feet above normal flood level along the major streams of the region (Reed 1952). Narrow leaf cottonwood (*Populus angustifolia*) is the dominant tree but blue spruce (*Picea pungens*) also occurs. The shrub stratum consists of *Salix* spp., *Ribes* spp., *Rosa woodsii,* and others. The herb stratum contains many species of grasses (*Poa pratensis, Bromus ciliatus, Bromus inermis,* and others) and forbs (*Fragaria glauca, Delphinium nelsoni, Aster* spp., *Gentiana* spp., and others). The soil is moderately deep and somewhat moist throughout the year. There seems to be a general correlation between the size of the mounds formed by pocket gophers and the depth, moisture content, and rockiness of the soil (Laycock 1952). In relatively deep, non-rocky, moist (not water-logged) soils, such as in this community, the gophers often form large aggregate mounds up to 5 feet in diameter and 12 inches deep. In shallow, rocky, dry soils the gophers make very small, shallow mounds, usually less than 12 inches in diameter.

Aspen community

This community occurs in 2 phases, one on the flat, moist lower areas, and the other on the dry hillsides. Although Reed (1952) found significant floristic differences between these 2 phases, they were considered as only one community in the present study because the data were not segregated as to the 2 phases when collected and because of the similar gopher activity in both. Quaking aspen (*Populus tremuloides*) is the dominant with an understory of grasses (*Melica spectabilis, Poa pratensis, Bromus carinatus, Stipa columbiana,* and others) and tall, conspicuous forbs (*Aster integrifolius, Helianthella quinquenervis, Lupinus parviflorus, Osmorhiza* spp., *Senecio* spp., and others).

Results

There were 829 individual plants of 44 species growing through the mounds (Table I) and 1115 plants of 19 species growing on the mounds (Table II). Of the 151 mounds which had plants growing in them, 135 had plants growing through them and 82 had plants growing on them. Sixteen mounds had only plants growing on them and no plants growing through them, while 69 mounds had only plants growing through them and no plants growing on them.

There was an average of 12.9 plants of both categories per mound for the total of 151 mounds in all communities. There was an average of 19.8 plants per mound for the 55 mounds in the streamside forest community, 9.8 per mound for the 53 mounds in the aspen community, and 7.8 per mound for the 43 mounds in the big sagebrush community.

Plants growing through mounds

Thirty (68.2%) of the 44 species growing through the mounds are hemicryptophytes, 5 species (11.4%) are therophytes, 4 species (9.1%) are geophytes, 3 species (6.8%) are chamaephytes, and 2 species (4.5%) are phanerophytes (Table III). The largest total number of individual plants (625 or 76.3% of the total) and the largest number of individual plants growing through the mounds in all 3 communities are also hemicryptophytes (Table I). The second largest number of total individual plants (112 or 13.5%) and the second largest number of plants growing through the mounds in the streamside forest and the aspen communities are geophytes, however theorophytes are the second highest in number in the big sagebrush community. Phanerophytes and chamaephytes are very poorly represented in all communities. Table III compares life form spectra based on numbers of species and life form spectra based on total numbers of individual plants. The percentage of hemicryptophytes based on individual plants growing through the mounds is slightly higher and the percentages of phanerophytes, chamaephytes, geophytes, and therophytes are slightly lower than the corresponding figures based on the number of species but the differences are not of large magnitude.

There was an average of 6.1 plants for each of the 135 mounds which had plants growing through them. There was an average of 9.6 plants growing through each mound having plants of this category in the aspen community, 4.9 per

TABLE I. Plants growing through the mounds in the 3 communities

	Number of Individual Plants in each Community			
	Big Sagebrush	Streamside Forest	Aspen	Total
THEROPHYTES				
Epilobium paniculatum	14	....	4	18
Orthocarpus luteus	14	....	1	15
Thlaspi arvense	....	14	....	14
2 other species*	4	1	11	16
Total THEROPHYTES	32	15	16	63
Percentage of total plants	22.1%	7.4%	3.3%	7.6%
HEMICRYPTOPHYTES				
Taraxacum officinale	16	14	74	104
Fragaria glauca	14	48	49	101
Phleum pratense	35	....	44	79
Galium boreale	....	3	55	58
Solidago spp.	....	27	26	53
Achillea millefolium	2	5	27	34
Trifolium rydbergii	....	25	....	25
Poa pratensis	....	1	23	24
Festuca idahoensis	....	....	23	23
Senecio spp.	....	18	....	18
Thalictrum occidentale	....	1	13	14
Lupinus parviflorus	....	....	12	12
Aster spp.	7	2	2	11
17 other species*	21	20	38	79
Total HEMICRYPTOPHYTES	95	164	376	635
Percentage of total plants	65.5%	80.4%	78.3%	76.6%
GEOPHYTES				
Bromus inermis	....	13	68	81
Agropyron dasystachyum	5	5	16	26
2 other species*	1	2	2	5
Total GEOPHYTES	6	20	86	112
Percentage of total plants	4.1%	9.8%	17.9%	13.5%
PHANEROPHYTES				
Rosa woodsii	....	4	1	5
Artemisia tridentata	2	....	....	2
Total PHANEROPHYTES	2	4	1	7
Percentage of total plants	1.1%	1.9%	0.2%	0.8%
CHAMAEPHYTES				
Artemisia frigida	9	....	....	9
Artemisia ludoviciana	1	1	....	2
Arctostaphyllos uva-ursi	....	....	1	1
Total CHAMAEPHYTES	10	1	1	12
Percentage of total plants	6.9%	0.5%	0.2%	1.5%
TOTAL PLANTS	145	204	480	829
Number of mounds with plants growing through them	43	42	50	135
Average plants per mound	3.4	4.9	9.6	6.1

*Other species with 10 or fewer plants are; Therophytes—*Androsace septentrionalis* and *Polygonum englemanii;* Hemicryptophytes *Eriogonum subalpinum, Poa fendleriana, Geranium nervosum, Agoseris* spp., *Potentilla* spp., *Stipa columbiana, Collomia linearis, Bromus marginatus, Carex* spp., *Arabis* spp., *Koeleria cristata, Lomatium ambiguum, Bromus ciliatus, Rumex* spp., *Gentiana* spp., *Sitanion hystrix* and *Swertia radiata;* Geophytes—*Equisetum hiemale* and *Melica spectabilis.*

TABLE II. Plants growing on the mounds in the 3 communities

	Number of Individual Plants in each Community			
	Big Sagebrush	Streamside Forest	Aspen	Total
THEROPHYTES				
Muhlenbergia filiformis	....	*	....	*
Thlaspi arvense	....	722	....	722
Polygonum englemanii	184	86	14	284
Androsace septentrionalis	....	27	11	38
Collomia linearis	....	18	....	18
2 other species‡	....	....	5	5
Total THEROPHYTES	184	853†	30	1,067†
Percentage of total plants	97.4%	96.4%	73.2%	95.7%
HEMICRYPTOPHYTES				
Senecio spp.	....	19	....	19
Galium boreale	....	1	4	5
Phleum pratense	4	....	1	5
7 other species‡	1	6	6	13
Total HEMICRYPTOPHYTES	5	26	11	42
Percentage of total plants	2.6%	2.9%	26.8%	3.8%
GEOPHYTES				
Bromus inermis	....	5	....	5
Agropyron dasystachyum	....	1	....	1
Total GEOPHYTES	....	6	....	6
Percentage of total plants	....	0.7%	....	0.5%
TOTAL PLANTS	189	885†	41	1,115†
Number of mounds with plants growing on them	23	41	18	82
Average plants per mound	8.2	21.6	2.3	13.6

*Ten mounds in the streamside forest community had an estimated ground cover of 5% of *Muhlenbergia filiformis.*

†Totals exclusive of *Muhlenbergia filiformis.*

‡Other species with less than 5 plants each are; Therophytes—*Chenopodium album* and *Orthocarpus luteus;* Hemicryptophytes—*Bromus ciliatus, Lomatium ambiguum, Solidago* spp., *Achillea millefolium, Agoseris glauca, Gentiana* spp., and *Poa pratensis.*

TABLE III. Comparison of life form spectra based on numbers of species and life form spectra based on total numbers of individuals plants

Life Form Spectra	Ph	Ch	He	Ge	Th
Plants growing through the mounds					
Based on numbers of species	4.5%	6.8%	68.2%	9.1%	11.4%
Based on total numbers of individual plants	0.8%	1.5%	76.6%	13.5%	7.6%
Plants growing on the mounds					
Based on numbers of species	0	0	52.6%	10.6%	36.8%
Based on total numbers of individual plants	0	0	3.8%	0.5%	95.7%

mound in the streamside forest community, and 3.4 per mound in the big sagebrush community (Table I).

Taraxacum officinale and *Fragaria glauca* are the most abundant species growing through the mounds and *Bromus inermis, Phleum pratense,* and *Galium boreale* are the next most numerous species. *Phleum pratense, Taraxacum officinale,* and *Fragaria glauca* are the most abundant species in this category in the big sagebrush community, and *Fragaria glauca, Solidago* spp., and *Trifolium rydbergii* are the most abundant species in the streamside forest community. *Taraxacum offici-*

nale, Bromus inermis, and *Galium boreale* are the most abundant species growing through the mounds in the aspen community. Table I lists the numbers of all individual plants of each species growing through the mounds in the 3 communities.

Plants growing on mounds

Ten (52.6%) of the 19 species of plants growing on the mounds are hemicryptophytes, 7 species (36.8%) are therophytes, and 2 species (10.6%) are geophytes (Table III). The greatest number of total individual plants (1067 or 95.7% of the total) are therophytes and this life form includes 73.2 to 97.4 per cent of the individual plants in all 3 communities (Table II). Hemicryptophytes are the second most abundant in all communities and there are a few geophytes only in the streamside forest community. Table III compares life form spectra based on numbers of species and life form spectra based on total numbers of individual plants growing on the mounds. As indicated above, hemicryptophytes make up the largest percentage of the life form spectra based on numbers of species but therophytes make an extremely large percentage (95.7%) of the life form spectra based on total individual plants.

The figures for therophytes in the streamside forest community do not include counts of *Muhlenbergia fililformis,* which was found growing on 10 mounds in this community. The size of the mounds varied from 1.5 feet to 5 feet in diameter and this annual grass covered approximately 5 percent of the surface of these mounds. The total number and percentages of therophytes growing on the mounds would be much higher than the figures given if actual counts of this grass had been made.

There was an average of 13.6 plants for each of the 82 mounds which had plants growing on them. There was an average fo 21.6 plants growing on each of the mounds which had plants of this category in the streamside forest community, 8.2 per mound in the big sagebrush community, and 2.3 in the aspen community.

Although no definite counts were made of *Muhlenbergia filiformis,* this species makes up the largest total number of plants growing on the mounds and *Thlaspi arvense* and *Polygonum englemanii* are the next most abundant species. *Polygonum englemanii* is the most abundant species growing on the mounds in the big sagebrush community and *Muhlenbergia filiformis* and *Thlaspi arvense* are the most numerous species in the streamside forest community. *Polygonum englemanii* and *Androsace septentrionalis* are the most abundant species growing on the mounds in the aspen community. Table II lists the numbers of individual plants of each species growing on the mounds in the 3 communities.

Discussion

It is evident that both categories of plants, those growing through the mounds and those growing on the mounds, are important in the initial revegetation of pocket gopher mounds in this area. The present study was not extensive enough to determine which category is more important, if one is more important than the other. There were more individual plants growing on the mounds than growing through them, but there were considerably more mounds with plants growing through them than mounds with plants growing on them.

Ellison (1946) pointed out that gopher mounds in uneroded areas with a good plant cover make relatively poor seed beds. The rather low average number of plants growing on the mounds in the big sagebrush and aspen communities supports this conclusion, but, on the contrary, the average number of plants growing on the mounds in the streamside forest community (Table II) is relatively high. The soil in the streamside forest is moist (but not too wet for gopher activity) throughout the summer and this moist condition evidently makes the soil of the mounds a good seed bed. The soil in the other communities is fairly dry at least part of the summer and probably is too dry for seed germination. This dry condition of the soil of the gopher mounds may partially explain why such a small proportion of mounds have plants growing on them.

The very high percentage of therophytes based on total individual plants growing on the mounds (Table III) shows very clearly that it is these plants, the annuals, which contribute most to this phase of revegetation. The seed bed conditions of the mounds are more favorable for therophytes than for any other life form, but the number of species of therophytes in the region is limited. This results in a much higher percentage of therophytes based on total individual plants than the percentage based on number of species. It is not known whether the plants growing on the mound start mainly from seeds already present in the soil when it was pushed up in the mound or from seeds deposited in the mound after it was formed. Beetle (1955) reported that rodent disturbance offers a ready entrance for sagebrush seedlings into grassland areas. Sagebrush seeds do not germinate under the normal litter of grassland because they require considerable light, but they do germinate in the exposed soil of gopher mounds. However, no sagebrush seedlings were found growing on the mounds in this study.

The differences between the percentages of life forms based on numbers of species of plants growing through the mounds and the life form spectra based on total numbers of individual plants (Table III) vary much less for each life form than the corresponding figures based on plants growing on the mounds. The plants which are established in the community are the ones which grow through the mounds. As hemicryptophytes probably make up the largest part of the flora of Jackson Hole they would be expected to, and do, make up the largest percentage of plants which grow through the mounds. Perhaps an additional explanation for the predominance of hemicryptophytes in the plants growing through the mounds is that hemicryptophytes are probably the best suited of all life forms to survive the covering of the soil of the mound. The perennating organs of hemicryptophytes are just below the surface of the soil. When they are covered with the soil of the mound the re-orientation of the bud to the new soil surface level (the top of the mound) is a relatively minor adjustment unless the mound is very thick. The thickness of the mound, of course, influences the number and kind of plants which are able to grow through it. The degree of this influence was not determined in the present study.

The consideration of the plants growing through the mound as simply a re-orientation of the perennating organs of the hemicryptophytes emphasizes the point that the 2 categories of plants involved in mound revegetation are actually 2 different phases of revegetation or 2 types of micro-secondary succession. The plants which grow through the mounds are the former occupants of the site re-asserting themselves but the plants which grow on the mound are new to the micro-site (the individual gopher mound). In areas where the pocket gopher is part of the natural biotic community the gopher mounds are small areas where pioneer species, the therophytes, are continually perpetuated. Thus stable or "climax" communities as well as disturbed areas will always include pioneer species as well as the so-called "climax species." If the gopher population is small these therophytes may be a very small part of the total vegetation, but if the population is large the therophytes may make up a significant part of the vegetation of a community and will be included in any representative sample of the community. This study did not reveal what plants succeed the therophytes at a given micro-site.

The amount of the variation in the average number of plants growing through the mounds in the 3 communities probably can be attributed to the differences in the amount of ground cover in the 3 communities. The open portion of the aspen community undoubtedly has the highest percentage of ground cover by plants and consequently has the highest average number of plants growing through the mounds (Table I). The big sagebrush community probably has the lowest percentage of ground cover by plants and has the lowest number of plants growing through the mounds.

There are many factors which may influence the kind and quantity of plants which grow through the gopher mounds. Weaver and Fitzpatrick (1934) noted that most prairie species are killed when covered by gopher mounds but that some of the tall grasses may push through the soil near the edge of the mound and actually grow more luxuriantly due to the increased moisture. Aldous (1951) made a study of the feeding habits of gophers in Utah and found that gophers clip and remove all vegetation within an 8 inch radius from the tunnel before depositing any soil on the surface. Ellison (1946) and Moore and Reid (1951) state that at least some plants are killed by being covered by the soil of the mound. Perhaps this partially explains why such a large proportion of mounds have no plants growing through them. The clipping, when it occurs, followed by the covering of soil probably makes it impossible for many plants to survive and grow through the mound. Ellison (1946) also reported that in areas where patches of vegetation alternate with bare soil, the gophers tend to cast the soil of the mound into the bare spaces between the patches of vegetation. The 3 communities studied had a fairly uniform plant cover so this tendency was not noted.

The present study was not intended to be a complete study of the revegetation of gopher mounds, however it does give an indication of the first stages of revegetation. Additional work on this subject is needed to determine the full extent of the influence of the pocket gopher on vegetation.

SUMMARY

(1) The purpose of the present study was to determine what plants are the first to occupy the pocket gopher mounds in the vicinity of the Jackson Hole Wildlife Park, Wyoming.

(2) Plants growing in the mounds in 3 communities were assigned to 2 categories: plants growing through the mounds, i.e., those which had survived being covered by soil and had grown

through the mound, and plants growing on the mounds, i.e., those which started from seed in the mounds. The species were further grouped according to the life form classification of Raunkiaer.

(3) The greatest numbers of species and the greatest numbers of total individual plants growing through the mounds are hemicryptophytes. *Taraxacum officinale, Fragaria glauca, Bromus inermis, Phleum pratense,* and *Galium boreale* are the most abundant species growing through the mounds.

(4) The greatest numbers of species growing on the mounds are hemicryptophytes, but the largest numbers of individual plants are therophytes. *Muhlenbergia filiformis, Thlaspi arvensi,* and *Polygonum englemanii* are the most abundant species growing on the mounds.

(5) The average number of plants growing on the mounds in the streamside forest community is much higher than the average in the other 2 communities, probably because the soil is moist throughout the summer, while the soil of the mounds in the other communities is too dry for good seed germination part of the summer.

(6) Both categories of plants are important in the initial revegetation of gopher mounds in this area.

(7) Where the pocket gopher is part of the biotic community the gopher mounds are microsites where pioneer species (therophytes) are continually perpetuated. Thus, stable or "climax" communities as well as disturbed areas will always include these pioneer species.

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NOTES AND COMMENT

PLANT ECOLOGY AS A BRANCH OF BOTANY

The Problem Under Discussion

Plant ecology and plant geography are parts of botany, but details of the relationships among these three categories of plant study are not always universally agreed upon. There is obvious overlap and inclusion. Disagreement may be expected even more in the New World than in Europe since these studies were transplanted here without bringing along the traditions on which they were based. In addition to tradition, training, interest, and other personal proclivities may have as much to do with the title given to a study as a logical analysis of its content and aims.

Even analyses can differ. For example, a recent paper by McMillan (1956) on the status of plant ecology and plant geography invites discussion. It and a backlog of other papers limit or extend the scope of ecology without regard to previous and perhaps more logical organizations of botanical facts. The purpose of my paper is not to emphasize disagreements with other ideas but to begin a discussion whose continuation will clarify those plant ecological concepts on which botanists do universally agree. Such agreement is basic for science (Campbell 1920).

As prefatory remarks I stress that plant ecology and plant geography are international sciences. Should it really be necessary to qualify any science in this way? Vegetation will be considered. For "causality" in relating plants to environments is substituted "functional relation." We can answer the question how plants are related to their environments whereas why they are related is much more problematic. The question "why?" has usually given way to the question "how?" before scientific progress has been made (Burtt 1932).

Appreciated comments on this paper have been made by members of the seminar in ecology of the University of California, especially by H. F. Heady and J. M. Tucker. F. E. Egler has also helpfully criticized it. However, their agreement with its present form should not be assumed.

Definitions of Plant Ecology and Plant Geography

Historically, original and accepted definitions of terms have a certain significance besides their intrinsic value of fixing particular concepts. They are the foci from which later definitions have radiated and evolved. While new definitions can be highly valuable, to preserve continuity of understanding the new concepts or rearrangements of old concepts which they introduce should be related to those prior definitions under which a science has developed.

Plant ecology was originally defined by Haeckel (1866: I, p. 238; II, pp. 286-289) as the relations of plants with their environments, and it has been used in this sense often and subsequently by Tschulok (1910), Diels (1908, 1945), DuRietz (1921), Rübel (1922, 1927, 1930), del Villar (1929), Braun-Blanquet (1928, 1932, 1951), Egler (1942), Daubenmire (1947), Oosting (1956), Stocker (1952), Walter (1949-1951), Tansley (1954), etc. The literature mentioned bounds and illuminates the subject of plant ecology in a usable way. From filling in a gap in physiological researches, as many have envisaged it, ecology has developed its own unique principles, mainly as it included the study of vegetation or plant sociology.

As treated by Diels (1908), plant geography included floristic, ecologic, and genetic relations of plants to the earth's surface. Diels systematized in this way the contents of DeCandolle's earlier summary of plant geography (1855). This broad, earth-directed usage is still general (Diels 1945, Raup 1942: 346, Cain 1944, Good 1953, Meusel 1954, Wulff 1943, Alechin 1950, Sukachev 1950, Carles 1948, Gaussen 1954, del Villar 1929). Plant geography was, and is, a subject broader in scope than plant ecology, preceded the latter in development, and gave rise to plant ecology through an elaboration of one of its aspects by Schimper, Warming, and others, at about the turn of the century. It gave rise to "plant ecology"—an American and British usage. On the continent, plant geography was not so unceremoniously verbally abandoned, and floristic botany was giving rise to plant sociology, which did not neglect ecology as one of its viewpoints (see below).

From the definitions and usages given above, ecology is simply an elaborated part of plant geography. We can endeavor, however, to point out more fundamental differences.

Distinctions Between Plant Ecology and Plant Geography

Conceptually we can separate the relations of plants to environment from their relations to the earth's surface. That an environment occupies an area is a secondary consideration. Environment and station are not synonymous.

As to methodology, plant ecology is a study which can be carried out in the field or even under artificial, experimental, or controlled conditions in laboratory, greenhouse, or garden. Quantitative expression of general functional relationships to environment can result. On the other hand, the study of plant geography is basically observational. Its results can be mapped. They are not functional expressions.

The etymology of the word "geography" (earth + description) is instructive, especially as compared with the related subject geology (earth + word, speech, reason, science by extension). Ecology shares the root *logos.*

In plant geography we always consider the earth; in plant ecology such terrestrial relationships are not stressed. Plant geography is an earth science, but ecology as a concept is not defined in relation to any particular part of the earth.

The concept ecosystem, for example, is environmental or ecological. It may be equated to Sukachev's idea of biogeocoenose. As Sukachev (1945, 1950: 462) says, the biogeocoenose and the element of geographic landscape are not identical. The taxonomic unit of the latter, geographical study may include several biogeocoenoses which differ in kinds of plants and kinds of habitats. The geographical category landscape refers to a unit regional territory. The biogeocoenose is not defined in this way but is an ecological unit. As Tolmachev phrases it (1953: 329): "The biogeocoenose exists not in a given locality (a part of the earth's surface) but in a given environment, in the formation of which it has taken part." The distinction between geographical locality and environmental habitat was early expressed by Gams, Pavillard, del Villar (1929: 15), Braun-Blanquet (1928: 19), and Yapp (1922) among others. The point to be made is that such a distinction has been made so repeatedly that we must conclude plant geography and ecology need not be one and the same study. Plant geography concentrates first on locality; plant ecology concentrates on relations between plant and environment.

To this point we have used "ecology" to cover either its inclusive Anglo-American meaning or its European sense as a viewpoint which forms a part of the study of either individual plants or of plant communities. The usual American employment of the term ecology to include the study of vegetation is obviously illogical. Phytosociology is a more apt term, although some would give it anthropic connotations. Phytocoenology would seem to be least objectionable.

The difference between plant sociological and plant geographical aims is clarified by certain criticisms of the former. Egler (1942: 248-9, 1954: 48-9) and Paffen (1951) both complain that the results of at least the Zürich-Montpellier kind of plant sociology yield no idea of the landscape pattern of vegetation. From the descriptive and analytical data in a plant sociological monograph of a given region, one can form no mental picture of the plant geographical distribution of the vegetation. This is true even when the monograph contains, as most do, excellent discussions of the structure and composition, ecology, distribution, functioning, genesis, probably even history of the vegetation being described. But why should plant sociological data automatically give a plant geographical synthesis? To expect it is simply to confuse the objects of study of plant sociology (including ecology) and plant geography, that is, plant communities and individual plants on the one hand, and the botanical aspects of landscapes on the other. The phytosociologist provides the raw material of plant association descriptions and analyses which the geographer can then organize into landscape patterns. Descriptions of vegetation units, continua, or sequences is a first step for their geographic study. The other data of plant sociology besides the purely descriptive are necessary for geographical understanding. Regel (1949) reviews the difference between plant communities as phytosociological units and landscapes as geographical units.

Obviously, since both individual plants and vegetation occupy area, ecological and phytosociological studies have some point in common with plant geographical studies. Thienemann (1941: 324) says that geography treats of space and, therefore, impinges on ecology. The intersection of geography with ecology has been a perennial source of confusion for plant ecologists—most recently in McMillan's (1956) discussion I believe—as well as for evolutionists' treatments of ecological and geographical isolation, clarified by Cain (1953) and Stebbins (1950). Obviously, the ecosystem and biogeocoenose have some spatial connotation. They are, therefore, partially geographic. In them ecological and geographical points of view intersect—which is not to say that they coincide.

In general the areal scales of study in plant ecology and sociology and plant geography differ by a factor of at least 10 to 100. If the ecologist or phytosociologist maps quadrats on a scale of 1/10 to 1/100 or plant communities at 1/5,000 to 1/20,000, the plant geographer may use mapping scales of 1/200,000 or even smaller. Would either ecologists and phytosociologists or plant geographers agree to this distinction?

Evidently then there is no absolute difference between ecological or phytosociological and geographical mapping of either plant taxa or vegetation. There is this difference in scale. The point is illustrated abundantly and excellently by Meusel (1943). His local maps of species distribution, done to a large scale, illustrate the ecology of the species; his maps of continent-wide species distribution, done to a small scale, illustrate primarily the geographical relations of the species and only the grosser aspects of their ecology. Meusel, then, illustrates one of the differences in results between the usually more extensive study of plant geography and the more intensive, and limited, ones of plant ecology and sociology. The objectives by their choice of quantitative scale determine the qualitative kind of results. The difference in scale does not itself determine whether a study is ecological or geographical. The type of data which inevitably results from the use of one scale or another does determine the nature of the study.

In summary, there are two differences between plant ecology and plant geography: 1) A theoretical difference, since plant geography is concerned with the relations of plants to the earth and not to environment as such, and 2) A practical difference, since the relative scale of study usually differs, partly, at least, as a consequence of the first point.

Ecology as a Point of View

Granted that plant geographers study the terrestrial relationships of plants and ecologists their environmental relationships, this still does not place ecology very precisely within the field of botany. Ecology could be, and has been, considered encyclopedic and embracing almost all of botany or ignored as already included in other botanical studies, as treating individual plants or vegetation, as floristic or physiognomic, as classificatory or causal, as descriptive or experimental, etc. The following section aims to locate ecology among other botanical disciplines—to show its place, scope and limitations.

We focus on the general studies of ecology and phytosociology in this paper, rather than the systematic study of plant geography. The basic position of systematic studies for generalizations is recognized, but it was precisely because plant geography was an ungeneralized mass of information that ecology and plant sociology arose. There is no intent of underestimating the value for plant ecology and sociology of the floristic data which are usually supplied by plant geographers. The large- and small-scale distribution of a taxon is probably its most apparent autecological property; definition of the flora contributing to a particular stand of vegetation is the first task of the phytosociologist. Still the viewpoints of the two subjects are different, and this paper attempts to place plant ecology in botany. We desire neither the omission of any logical place for plant geography nor the immersion of ecology in it.

Tschulok (1910) in a study of the bases of biology suggested a general division of any scientific study dealing with natural phenomena. Tschulok's scheme has been used partially by many (Odum 1953, McMillan 1956, e.g.) in defining the status of plant ecology. There may be advantages in using the original. Tschulok, then, describes eight incommeasurable points of view which can be applied to the study of biological objects. These points of view have already been related to plants by Egler

(1942); the present discussion is intended only to supplement Egler's fundamental treatment of the subjects of botanical study.

This scheme of Tschulok's is particularly important because it indicates the place of ecology in biological investigations. It defines, limits, and indicates the value of the study of ecology.

Tschulok's points of view or approaches to study include:

1) Composition—the substances of which the plant, for example, is made;
2) Structure—arrangement of these units of composition, resulting in form;
3) Physiology—functions or life processes of the plant and its parts;
4) Genetics—origin of the plant from previous plants;
5) Ecology—relations of the plant to its environment;
6) History—past events related to the plant;
7) Chorology—distribution on the earth;
8) Taxonomy—classification.

In Table I is suggested a system of botany along these lines. References to similar presentations are given by Egler (1942: 256). Becking (1957: 467) gives a variant.

TABLE I. A partial system of botany, emphasizing the difference between studies of individual plants and of plant communities. Modified from DuRietz (1921:28), Rübel (1927), del Villar (1929:22), Egler (1942:258), etc. The application to zoology should be direct.

	OBJECTS OF INVESTIGATION	
Empirical unit:	Individual plant, population	Stand of vegetation
The abstract unit:	Taxon, biotype, ectotype, subspecies, species	Plant community, phytocoenose, association, plant aspects of ecosystem or biogeocoenose
Generic name:	Flora	Vegetation
The study:	(Idio-) Botany, "floristic botany" (Egler 1942; 255)	Plant sociology, phytocoenology, Vegetationskunde.
	POINTS OF VIEW	
1. Composition	Biochemistry	Stand, community, and vegetation composition
2. Structure	Morphology; including internal anatomy, cytology, etc.	Stand, etc. structure
3. Functions, life processes	Physiology	Stand, etc. physiology
4. Genesis	Evolution	Plant succession, syndynamics
5. Environmental relations	Autecology	Synecology
6. History	Paleobotany	Paleobotany of Vegetation, chronological phytosociology, synchronology
7. Distribution in space	Chorology	Vegetation mapping, synchorology (DuRietz)
8. Classification	Taxonomy	Classification of vegetation, Gesellschaftssystematik.

Botany, according to this scheme, includes the study of individual plants, collectively the flora, plus the study of stands of vegetation, collectively vegetation. Certain theoretical entities enter into the discussion. These, if they yield predictions, are useful; their existence is irrelevant. They are products of that powerful human ability to generalize.

Flora and vegetation are examples of such generalizations. These aspects of the plant world were separated as objects of botanical study in 1849 by Thurmann in a form which is still useful. "The *flora* of a region is an enumeration of all the species which grow there, envisaged in a manner purely taxonomic or descriptive and independent of the abundance of each species. The rare plant occupies no less place than the common one. The number of species in the region forms a whole, considered in an abstract manner.

"The *vegetation* of a region is the plant cover which clothes it. It is formed of the species of the flora associated in diverse quantities and proportions; one plays a considerable role, others are scattered and lost in the mass. The former makes up a principal element of the natural scene which the country offers. The latter often occupy only a minimal place.

"To know thoroughly the vegetation it is necessary to know the flora, but one can have studied the flora without rendering an exact and complete account of the vegetation. The flora of a country and its vegetation are therefore two different things which must not be confounded. The first encompasses only the number of distinct plant forms which one observes there, the second their proportions and their association."

Vegetation is thus composed of associations of plants. It represents the order with which plants occur. If there were no such order, there would be no plant sociology—no study of vegetation.

The concrete stand of vegetation is the basic unit for the study of vegetation (Braun-Blanquet 1928, 1932, 1951) or phytocoenology (Sukachev 1950: 452). The stand is an existing piece of vegetation. It is a grouping of individual plants to form a botanical individual of a new kind. When such recognizable groupings re-occur, they can be abstracted into a kind of plant community. Sukachev (1950: 452-3) has an admirably clear discussion of the two kinds of units heading the flora and vegetation columns of Table I.

It should be noted that the "abstract" terms in this table have the usual double meaning of abstract and concrete. One of our mental abilities is the capacity to make generalizations from our concrete experience, and we frequently do not differentiate between the abstract and the concrete meaning.

An abstract plant community can be of any taxonomic rank, of course.

Egler (1942: 248-9) believes that, on the basis of existing literature, plant communities and vegetation are on two different levels of integration. Under this view, plant community study is not vegetation study. Individual plants have somewhat the same relationship to plant communities as plant communities do to vegetation. The writer believes this usage of "vegetation" is in a geographical sense. We shall not use "vegetation" in this way but as the general term describing all the hierarchy of plant communities into which stands of vegetation are organized.

"Population" is a concept which bridges between the study of individual plants and of vegetation. A population is an interbreeding group of individuals which behaves in this way because of a temporal-spatial, and ecological, relationship between the individuals. The ecological framework is a stand of vegetation. A population is a part of a stand of vegetation. Its limits do not seem to be definable except in relation to vegetation units. A population is not normally simply the contents of a herbarium folder unless the exsiccatae came from a defined piece or kind of vegetation.

As to the dynamism of the points of view, this is a minor point. Studies of composition and structure can be static, but they can be dynamic as in reaction and developmental studies. The processes involved in functions and genesis are by nature dynamic. The relationships expressed by the remaining points of view are dynamic by nature where time itself is involved or dynamic by choice if time is considered as a factor. Certainly dynamism in vegetation is not limited to plant succession (Becking 1957: 467). In any case static descriptions are prerequisite for dynamic study.

Composition has been added to Tschulok's original seven points of view in agreement with Egler (1942: 257). This accommodates for the study of individual plants both biochemistry, including some of its structural aspects, and some parts of histology. When considering vegetation, composition is the list of species making up the studied stands.

Such records of stand surveys (Aufnahmen, relevés) are the basic data of plant sociology. They document the studies of morphology and structure, of ecology, physiology, genesis, history, chorology, and classification. As this literature grows, comparisons and re-interpretations are becoming possible. It is quite obvious that the original taxonomic arrangement of stand surveys into association tables, continua, gradients, functions, or sequences is merely a working hypothesis. So too are other arrangements. Unless these stand surveys become part of the literature, the data of a vegetation study will disappear along with their interpretation as the interpretation becomes obsolete.

Egler regarded genetics of individual plants as a part of physiology, and genesis of vegetation as part of the study of composition. However, heredity and variation combine in the study of evolution as a distinct science for individual plants, only incidentally treating the physiology of reproduction (Stebbins 1950). "Ontogeny" has not been used there for the genesis of units of the flora because the word refers to development of an individual, not a taxon of some rank.

The evolution of plant communities occupies a similar, discrete position in the study of vegetation (Major 1951). There is no conflict here with DuRietz' (1921) classification of plant succession as a part of paleobotany since he took this term in the then-current Clementsian meaning which related vegetation development to the monoclimax and, therefore, to peneplanation, base leveling, physiographic erasure of local climatic differences, and similar processes involving changes in the independent features of the environment (Major 1951: 398). DuRietz accepted the autogenic development of vegetation, long ago studied by Kerner and other Europeans, and more recently regarded as a foundation of ecology by Cowles, Clements, and Tansley, as being the genesis of plant communities.

In the American vegetation literature plant succession and vegetation history have not been sharply differentiated. I am confining the term "plant succession" to those autogenic changes in vegetation which take place under constancy of the other independent factors of the environment besides time, and where the span of time involved is of an order of magnitude of hundreds of years (Major 1951: 398). History would then include those changes with time of greater order of magnitude and include changes in vegetation resulting from changes in the independent factors of the ecosystem. Braun-Blanquet (1951: 515) uses the terms "community development" or "syndynamics" for our plant succession and "community history" or "synchronology" for our vegetation history. Others have spoken of the ontogeny and phylogeny of vegetation. Lüdi (1932: 535) saw the necessity of recognizing these two different kinds of change of vegetation and named them actual and secular changes. Etter (1947: 153-157) also defined recent succession and secular or historical changes in vegetation and described their differences. For example, a succession is frequently repeated on one given area; historical changes are not, in general. Over the course of history the very factors which enter into an ecosystem change. New ecosystems result, not merely new time states of one ecosystem. Thus succession is predictable; historical change is not. Plant succession is subject to observation; historical changes in vegetation are not except as paleobotanical materials come to light. Yearly climatic fluctuations will confuse a successional trend or if intense and of decade duration will initiate new successions; such climatic fluctuations may simply mask a historical trend of change in vegetation. The units of vegetation involved in succession we can see about us and describe; the units of historical change are lost in the past. Clements, of course, invented the terms sere and clisere for these phenomena of genetic and chronological changes in vegetation. Tansley's terms "autogenic" and "allogenic" have much the same connotations.

Sukachev too (1944: 224, 227; 1950: 459-60) differentiates between syngenesis (succession) and coenogenesis (historical changes), with the latter divided into phylocoenogenesis and selectogenesis. Both of the latter change the available flora. In synecological study, vegetation may be taken as dependent on the factors of the ecosystem, and the flora is one of these independent factors determining vegetation (and soil). Changes in the flora result in historical changes in vegetation.

There definitely are several kinds of changes of vegetation with time. Cooper's (1926) grand "universality of vegetation change" can be refined.

At two places in Table I the same terms are notably *not* used for the same viewpoint applied to individual plants and to vegetation. First, 4. Genesis where evolution of individual plants sharply set off from succession of plant communities expresses the clear differences between ordinary biological organisms and units of vegetation. Second, 5. Ecology where Schröter's terms aut- and synecology reflect the growth of interest in plant ecology by Schröter himself and in plant sociology by his student Braun-Blanquet. That recognition of this usage of synecology accompanies no neglect of the ecological viewpoint is seen from Braun-Blanquet's Plant Sociology (1928, 1932, 1951). In successively larger editions the section on ecology has occupied 60, 59 and 45% of the total text.

The study of plant ecology in the English-speaking countries has taken over, by default I believe, in addition to its own subject matter not only the entire study of vegetation but also large parts of the historically older study of plant geography as well. This usage of "plant ecology" will be discussed later. The context will ordinarily clarify the sense, which is, after all, not one of absolute difference but rather one of degree of inclusiveness of subject matter.

Coming down to viewpoint 7 of Table I, the reader interested in the chorology of taxa is referred to Meusel's work (1943) for a splendid summary of data, ideas, methods, and results. Vegetation itself is even more commonly mapped than studied in applied ecology such as forestry and range management. This paradox simply means that different kinds of vegetation can be recognized, and under the pressure of necessity lines can be drawn on a map separating the different kinds. Close study is required to apply the other seven points of view, besides the chorologic one, to the recognized kinds of vegetation. Such detailed study has usually meant that the broad vegetation units recognized in a mapping program must be further subdivided in applied studies. Few complete monographs of vegetation units using all viewpoints have resulted. In any case, vegetation mapping requires a system of classification of vegetation unless we are to use an unordered set of terms, which would quickly become unmanageable.

A classification should be a summary, as well as an organization. As a summary it permits progress of a science; as an organization it ossifies it. Ellenberg (1956: 36) has recently clarified the bases and limitations of current classifications of vegetation: "Each person who makes a great number of vegetation stand surveys is impressed by three facts. He sees to his astonishment just how similar stands of plants can be under similar site conditons, even when they lie far apart geographically. By a closer comparison he also finds, however, that none of his stand surveys is exactly like another. Even neighboring stands on what are apparently the same kinds of sites differ from one another more or less. Now if he follows the same plant community over a large geographical area, he learns to recognize a third fact, namely that the species composition of this community changes more or less with the floras in the different regions. Thus the combination of species in plant communities is evidently regularly dependent on the environment; however, it is variable; and this variability is in principle unlimited because the stand is no organism." The many bases possible, and used, in classifying vegetation have been reviewed by Braun-Blanquet (1951: 553-561) and Ellenberg (1956: 37-99). Most of these coincide on analysis with a floristic classification based on characteristic and differential species. Of these indicator species, the ones most obviously suited to form the framework of a hierarchy of vegetation are the characteristic species, the constants and exclusives. We come back, then, in most systems of vegetation classification where both Tansley (1920) and Braun-Blanquet (1928, 1932, 1951) said we should have started—to the natural groupings of plants. The fact that, by the undisputed judgment of field botanists, there are natural groupings of plants is the only reason we have a science of vegetation, as Egler puts it.

We have attempted to define Tschulok's points of view as incommensurable, independent exercises, but obviously none of them is exclusive of the others. They are interdependent. All are necessary for complete understanding of plants. Tschulok also believed they were sufficient (1910: 196); no evidence or even opinion to date contradicts him.

The interdependence of Tschulok's 8 points of view is absolute. Not a single subject matter can stand or be pursued alone. The very broad scope of plant evolution provides a pregnant example (Stebbins 1950). Many of these points of view, such as ecology, physiology, genesis, history, and taxonomy are habitually thought of as syntheses.

Perhaps this interdependence is most striking when we consider taxonomy. Data from the other 7 points of view must be used to provide the most useful taxonomy. The workers in the various branches of botany need a classification, and each will provide his own if no one else does, but seven different classifications are not so good as one using data from all the possible seven.

Another view of taxonomy is that it studies phylogenies. This is reflected in McMillan's definition (1956) of taxonomy as investigating "How is this individual related to another individual?" It certainly requires data from all the eight points of view to establish a phylogeny, and this may be incorporated into a taxonomic scheme. At times, of course, phylogenetic data indicate no taxonomy along classical lines is possible. Apomicts, either facultative or obligate, and reticulate relationships expressed by introgression or hybridization are cases in point. McMillan's question can be taken to mean only that any classification produces classes which can be interpreted to indicate genetic relationships. Interpretations will vary.

McMillan points out that the last two of these eight points of view are frequently applied first. We first want to know the name of a new plant and where it occurs. Fortunately, taxonomy is concerned with more than nomenclature, but it has been altogether too unfortunately true that a minimum of knowledge about a plant, gathered from all the points of view, has sometimes accompanied its original naming. Extended synonymies reflect the painful correction of these gaps in knowledge. Logically taxonomy and chorology require data from the other points of view, but we shall accept the priority of taxonomy in botany and its intimate connection with chorology since at least Wettstein's day (1898). Chorology can be a subject in its own right, however, as shown by Meusel, Hultén, Böcher, Selander, etc., given a stable nomenclature. This is not true of taxonomy, unless it is only a system of nomenclature. Taxonomy can advance only so far and so rapidly as the other branches of botany provide it information. The re-births of taxonomy associated with plant exploration and more recently with the rise of genetics and ecology are illustrations (Stebbins 1950, Huxley 1940).

Tschulok (1910: 298-348) criticized the general botany texts of his time for neglecting several of these points of view, although botanists were in fact using them. Now textbooks seem to better reflect the activities of botanists. The Strassburger text in its 26th edition (Fitting, Schumacher, Harder, and Firbas 1954) is organized to treat botany as a whole. Morphology, physiology, and taxonomy still occupy most of the book, with composition introduced in morphology and physiology and with genetics appended to morphology. Firbas handles what Egler has called the fourth field of botany—the remaining plant geographical subjects of chorology, ecology, and history of plants—in the last few pages of this textbook. Stocker's review text (1952) is similarly organized, except that genetics is appended to physiology, and ecology is separated from geobotany.

Most American general botany texts are not so formally organized as the German ones and most neglect plant geography even more than do the classic texts. Frequently data from ecology, chorology, and history of plants are introduced, but usually as dressing, not as a fundamental part of the subject. Vegetation is simply not recognized as a subject matter separate from the study of individual plants.

On the other hand, the study of vegetation was systematically considered by Braun-Blanquet (1928, 1932, 1951) under Tschulok's points of view. They form the framework for a systematic treatment of plant sociology which has won wide acceptance. Paradoxically, Braun-Blanquet's ample section on ecology is usually taken out of context and appreciated more than his systematization of vegetation study, and his few pages on vegetation systematics have been confused with the objectives of phytosociology.

Rübel (1922, 1927, 1930) systematized geobotany around Tschulok's 8 points of view. He further applied them to vegetation, as well as to individual plants, as had DuRietz (1921) and later del Villar (1929: 22). If plant geography is taken in Diels' (1908, 1945) sense as including studies of the distribution, ecology, and genesis of floras and vegetation, its place in botany is quite clear. In Table I plant geography includes viewpoints 4 to 7; it is dependent, of course, on material from the other viewpoints. Rübel's system thus synthesizes much Swiss scholarship: Thurmann's clear separation of flora and vegetation, Tschulok's logical points of view, and Schröter's impetus to ecological study.

This systematic treatment of a subject according to points of view is not limited to botany. Besides flora and vegetation, we can apply these same points of view to soils, landscapes, and divisions of the animal kingdom. Of particular interest to botanists, who have long had an interest in plant geography, is the fact that both Berg (1947) and Troll (1950) used this scheme for geography, considered as the study of landscapes. The scheme seems to the writer to have quite general significance and to deserve complete statement, with active discussion if there is disagreement with it.

Examples of Applications of the Points of View to Individual Plants and to Vegetation

It is obvious that data derived from the 8 points of view as applied to individual plants (or generalized for species) are not identical even qualitatively to the data similarly derived for vegetation stands. The structure of a plant is different from that of a stand of vegetation. Similarly, measures of their life processes are different, and so on. Still the analogies are clear and illuminating. Such terms as morphology, physiology, genesis, ecology, paleontology, chorology, and taxonomy are not necessarily limited by their definitions to plants, to their parts, or to individual plants, or to biotic communities, or to ecosystems, or to geographic landscapes. These terms can be applied to any of these units without modifying their definitions. Operationally, data can be obtained which correspond to these viewpoints for any of the biologically important entities mentioned. Historically the terms have a wide biological meaning. To limit these terms to individuals is to ignore their meaning in biology and their 20th century usage.

Applying Tschulok's points of view to individual plants *and plant communities,* individual plants are composed of atoms, molecules, crystalline structures, and tissues; vegetation stands are composed of populations of plant species, better biotypes. Individual plants have a structure; so do vegetation stands as expressed by layering, extent of leaf surface, life form spectra. Individual plants function; there is a physiology of vegetation expressible by water and CO_2 relations of plant communities considered in their ecosystems (Huber 1952) and by yields of vegetation.

Note that none of these three functions of vegetation are predicted from data on the water and CO_2 exchange processes and yields of individual plants grown alone.

Plants grown alone are in a quite different environment from plants grown in a stand of vegetation. We would expect their physiological responses to be different, and they are (Ellenberg 1953 and 1956; Knapp 1954). The sum of the yields of individual plants growing in the identical environment as that provided by a given stand of vegetation should yield the same as the stand itself. Operationally, however, yield is more simply determined by harvesting a stand *in toto,* not plant by separate plant; and practically the environment provided by any stand of vegetation has not yet been completely described, much less reproduced. Of course, if the investigator's view is limited to individual plants, no data on the yields of plants under competitive conditions are possible. A great deal more study of plant communities must be made before we shall be in a position to describe even within what plant community our autecological yield data apply. Autecological studies must include the plant as it occurs competing with other plants in an association of plants (Ellenberg 1953, Knapp 1954, Clapham 1956).

In the case of gas exchange even the kind of summation we could theoretically make from absorption and release by individual plants to absorption and release by stands of vegetation is impossible because the plant community necessarily occupies area, and therefore, we cannot avoid including some of its habitat in these measures of the activity of the community itself. For example, in a plant community the CO_2 of the air is replenished by respiratory and other oxidative activities within the soil in a way which is not analogous to the activities of individual plants. As a matter of fact, the above-ground plant cover, with which we are usually necessarily concerned, fixes a net amount of CO_2; the soil releases a net amount of CO_2. The balance within the ecosystem may be quite complete, but quite different kinds of organisms are concerned in the plus and minus parts which together balance. A community of organisms is concerned; the activities of individual organisms are understandable only within this community framework.

Similarly, biological transpiration and physical evaporation both contribute to the water exchange of a stand of vegetation, but only transpiration is measured if the life processes concerned with water loss from individual plants growing alone are measured.

The argument that nothing happens physiologically except at the conceptual level of the individual (Mason and Stout 1954: 250) very severely restricts the definition of "physiology." This restriction to me seems quite arbitrary and to modify drastically the nature of physiology and its applications to organs, tissues, cells, etc. I conclude the term physiology may be applied to life processes anywhere in the organizational hierarchy of organic entities. In this hierarchy vegetation stands are at a higher level of generalization than are individual plants.

To continue: Individual plants have a genesis; vegetation stands do, also, and the name plant succession has been applied to the process. Autecology has been contrasted with synecology. Paleobotanical data for individual plants are matched by studies of the history of plant communities; for example, the work of Chaney and Mason on the Tertiary of western North America and Firbas' summary of the post-glacial forest history of central Europe. The geographical distributions of both individual plants and of plant communities are commonly mapped. Finally, both are classified.

Aberrations from the Ecological Viewpoint

A place for plant ecology and plant geography in botany is summarized above. A common and amazing perversion of Haeckel and Tschulok's use of the term plant ecology is perhaps best exemplified by Bonner and Galston's (1952) incorporating the subject matter into present-day plant physiology. However, their consideration of whole plants is slight, of any plant as it occurs in its natural or even normal ecosystem is minimal; and their data on environments are still more scanty. Perhaps it is invidious not to be grateful that an excellent textbook of plant physiology at least recognizes some of the problems of plant ecology and introduces the student to a few well-chosen results. The complaint is merely that study of plant ecology did not, and probably cannot, develop unless it be given specific and particular attention as the relations of plants to environments. This is not the usual definition of plant physiology. Unfortunately, Bonner and Galston make no attempt even to define the problem of environmental relations of plants so physiological data can be used in plant ecological study. Any presentation, such as theirs, which does not at least define the ecosystem in which the studied plants function and of which they form a part is certainly not ecological. Such studies are much over-simplified physiology as well (Parker 1946, Major 1951: 400-2).

Other dissents from usual views of ecology are expressed by McMillan (1956) and others. There are complaints that ecology is a potpourri of material from other disciplines. Could it be otherwise? I agree it would be more logical if American "ecology" did not include, besides the ecological study of individual plants as Tsuchulok used the term, also much of the plants' chorology, at least more recent paleobotany (palynological results), significant parts of genetics (Turesson 1922a, 1922b, 1926), and all the study of vegetation, including its ecology. Egler (1942: 259 and 1954: 49-50) has outlined the logical steps leading to some of this expansion by American ecology. Probably the taking over of palynology has been due to personal interests of the men who first exploited pollen analysis techniques, a desire to explore vegetation history in some more inductive and documented way (Godwin 1956) than by the deductive methods of plant distribution areas and Clementsian reconstructions in time, and the recognition that vegetation is a much better expression of climate than the occurrence or abundance of any single species of plant. Turesson's work on genotypical responses of plant species to habitats seems to have slipped smoothly into the system of phytosociological concepts prepared by Kerner's earlier equivalent data, intensively prosecuted floristic and taxonomic work, and Braun-Blanquet and his followers' sharpening of the indicator value of taxa through use of characteristic and differential species to discriminate plant communities. To the writer this expansion of autecology seems not aggrandizement but a natural effort to fill in gaps in botanists' training. That gaps exist is evident from McMillan's (1956) examination of the course work in ecology, or lack of it, offered by botany departments in state universities. Finally, of course, as Egler (1942, 1954) points out, American plant ecology has embraced the study of vegetation, but vegetation must be considered from all the 8 viewpoints of Tschulok's as noted above. In these viewpoints precedence must go to studies of structure and composition; although any science which does not also include studies of functions, genesis, ecology, distribution, history and crown these with a classification would be poor and incomplete indeed. As Becking (1957: 413) summarizes this matter, American "plant ecology" is too wide because it includes studies of environmental relations of both individual plants and of vegetation, and it is too narrow because it does not recognize in the study of vegetation applications of viewpoints in addition to the ecological.

Sukachev (1950: 461-2) discusses the heterogeneous nature of American ecology when it is made to cover not only autecology but all the study of vegetation. He would use "ecology" in the sense of Table I. He concludes that progress in vegetation study stops when it is included in "ecology," as in the United States and Great Britain.

Putting aside the peculiar field of American plant ecology, can any branch of science be other than a potpourri? Does any science stand alone? I believe these two questions really are facets of one. Scientific study has led to a more or less logical, more or less ordered view of the universe. The separate sciences are partial views, which depend on other sciences for completeness. Historically the various sciences have developed as offshoots from natural philosophy. None has become an independent entity. The writer can conceive of no science that does not rely on some knowledge of some communicable language and on logic and mathematics. Any botanical science must rely on chemistry and physics as well. Plant ecology must rely on the various divisions of botany and also those sciences whose subject matter is an aspect of the environment. The unification of plant ecology comes from its point of view (Tschulok 1910).

To study relationships we must have items to relate. Botanical science on the one hand provides plant data; the environmental sciences provide the environmental data. Normally botany does not tell us all that we as ecologists need to know about plants in order to be able to relate them to their environments. Even climatology, geomorphology, geology and petrology, pedology, anthropology, human history, organic evolution, floristics, zoology, and historical plant geography do not all together or separately give us the exact data on environments and the nature of our species that we as ecologists need. They ordinarily give us nothing on vegetation. It seems only normal to the writer that plant ecologists should draw from all these disciplines, and contribute to all. Ecologists' activities in this connection are merely an example of the interdependence of the points of view.

When the ecologist becomes an encyclopedist, it may be because his use of causation as a logical method has overwhelmed his sense of proportion. Causation is a classic infinite regress.

Birch (1955) has remarked the heterogeneous nature of ecology in a review of a recent general ecology text: "Here are some elements of ecology, physics, chemistry, plant physiology, animal physiology, pedology, oceanography and a little animal behavior (but no genetics). Perhaps ecology means a little of everything. The ecologist certainly sometimes feels like that, and most definitions of ecology and environment are so broad as to provide justification for such an approach. On the other hand we may believe it is time that ecology (like genetics) decided to become a more definitive science, instead of being the poor relation borrowing from all." If this is a criticism, it is understandable in view of Andrewartha and Birch's (1954) unique definition of ecology. They equate distribution and abundance to ecology. At least for plants these are not by any means all we would like to know about environmental relations. Very important quantitative aspects of plant growth are omitted. In different ecosystems these quantitatively variable plant characteristics determine success or failure in competition.

Also, at least for plants, we have no data showing that distribution and abundance are invariably only different aspects of the same phenomenon. Stenotopic plants such as *Oxyria digyna* (L.) Hill or *Lloydia serotina* Reichb. of circumpolar, arctic-alpine habitats or the vernal pool *Orcuttiae* and *Neostapfia* of the Great Valley of California may be nowhere abundant throughout their area of distribution for quite simple ecological reasons. They can grow nowhere but in rare and scattered habitats. Such plants, on the other hand, as *Scribneria bolanderi* (Thurb.) Hack. (Crampton 1955) and *Howelliella ovata* Rothm. (=*Antirrhinum ovatum* Eastw.) (Twisselman 1956) seem to have no ecological explanation for their widespread rarity. These two latter species occur throughout a considerable area, in rare stations, and even in those stations they are not abundant. Plants similar to the last are evident from Hulten's Atlas (1950). Examples are *Botrychium* spp. (except *B. lunaria* (L.) Sw.), *Athyrium crenatum* (Somf.) Rupr., *Carex bicolor* All., *Arenaria humifusa* Wahlenb., *Ranunculus hyperboreus* Rottb., *Draba crassifolia* Grah., *Potentilla emarginata* Pursh (=*P. hyparctica* Malte), *Oxytropis deflexa* (Pall.) DC, *Armeria maritima* (Mill.) Willd. ssp. *labradorica* (Wallr.) Hult., etc. Admittedly abundance is difficult to judge when the limiting area for showing single occurrences is 16 km. in diameter, but still the point is valid that, judging from Hulten's maps, for the plants mentioned distribution and abundance are not two aspects of the same thing. By regarding distribution and abundance as two facets of one phenomenon, Andrewartha and Birch have made ecology less of a potpourri by neglecting too much of it.

Nor can community ecologists be logically criticised, as they are by Andrewartha and Birch (1954: 4), for not producing enough autecologic data to satisfy the desires of students of life histories of individual species, or individual plants. They are community ecologists so they may study communities. Their primary interest is simply not "the distribution and number of animals in nature" but rather the communities which these organisms form. Indeed, Miller (1957) has recently maintained that ecology in general is mostly the study of communities.

Phytosociologists at least do not, as Andrewartha and Birch say community ecologists do (1954: 4), study habitats; rather they study recurrent groupings of more or less the same plant species. Such groupings have been shown to be excellent habitat indicators (Braun-Blanquet 1951), but this fact has followed their definition and study, not preceded it. These plant groupings are concrete realities. They are strictly empirical discoveries. Evidently the habitat does not have, or at least Andrewartha and Birch do not believe it can be defined to have, objective reality.

A danger of the habitat, and also ecosystem, approach is a tendency to define habitat so the plant's influences on the environment are not separated from measurements of that plant's environment. This makes the problem of ecology, namely a plant's environmental relationships, automatically unsolvable. If the functional relation of a plant to its environmental factors is set up so different but dependent properties of the same plant appear on both sides of the equation as unknowns, the equation is not solvable. For example, in the very simplest case, if the yield of a plant species is described as a function of the microclimate created by that same plant, we have found no general or even useful relationship between climate and yield of even the plant under consideration unless we have also at hand the functional relationship between the plant's microclimate and local or regional climate, which is not modified by the presence of the plant. In the latter case a parametric equation can be derived between yield and independent climate, but this relationship were better determined directly. It is necessary to define habitat in some way so dependent and independent variables can be separated for the analysis. The ecosystem and habitat can be fuzzy ideas if not cast into a functional form.

Plant ecology is sometimes defined as relating only to individual plants, as autecology. McMillan (1956) for example focuses on individual plants or taxa and mentions plant communities only as places where individuals occur. Unfortunately, Constance (1953) and Mason and Stout (1954) set a precedent for McMillan's treatment since they also omitted vegetation from consideration. They thus neglected an important aspect of the plant world and one which can greatly help biosystematic, physiological, morphological, and paleobotanical study. Applied botany is becoming more and more a study of vegetation. Without considering vegetation the study of environmental relationships of plants is operationally impossible.

By neglecting vegetation, the factor of competition is seemingly eliminated (Mason and Stout 1954: 255). By competition I mean simply that, when plants live together, they interact and so behave differently as compared to when they live alone, so far as we can measure. When growing together, different plants require the same things, which are often present in only limited supply. The plants interfere with one another; a reaction occurs in the lives of the plants. The term competition is thus a useful one; it is, of course, not very enlightening. However, giving a name to an unknown phenomenon is the usual way of starting to get it under control. As a matter of fact, no physiological data known to the writer have been able to explain why any particular plant grows naturally where it does without appealing to competition as a general term referring to the interrelations of plants. The reader is referred to the illuminating discussions of competition in plant sociology by Braun-Blanquet (1928, 1932, 1951) and to Ellenberg's evaluation of plant physiological data as they pertain to plant sociology (1950), leading to his nice differentiation of physiological and ecological tolerances of plants (1953). Recently Ellenberg (1956) and Knapp (1954) have summarized the work done to refine the concept of competition and give to it more operational and quantitative meaning in terms of physiological functions. Determination of these physiological functions is only a first step in studying competition.

Etymologically, "competition" describes quite precisely what seems to occur when plants live together. The word has no anthropocentric connotations; and some such general term is needed to describe the differences in behavior between plants growing alone and together.

Constance (1953) criticized American ecology, but omitted from his consideration vegetation. True, Constance was primarily concerned with individual plant systematics in discussng biosystematics, not vegetation systematics; but to ignore the potential help from synecology in defining individual plant habitats has resulted in also ignoring one of the important sources and kinds of variation in individual plants.

Clapham (1956) traced out many of the contributions to autecological understanding that derive only from the study of vegetation. Study of life histories of plant species clearly needs data from plant sociology.

In the writer's view McMillan (1956) has focused his attention only on those aspects of ecology which have long been almost exclusively the domain of the taxonomist. These include speciation, the sources of plant variability, and plant adaptations to habitats. The writer would be among the very first to agree that present taxonomy is inadequate for the ecologist's needs. However, this does not seem to justify jettisoning ecological problems in favor of taxonomic ones. In fact, one outstanding plant ecologist (Walter 1949-51:8) takes plant adaptations to environments as given. The source of genetically fixed adaptations to him is a genetic problem. The actual point of view which is plant ecology does not deserve neglect and neither does the entire subject matter of vegetation.

A Summary on Plant Geography

Plant geography has been discussed at several points in this paper. Originally plant geography encompassed the work on environmental relations of plants. Now there are real conceptual differences between the units of plant geograpical and plant ecological or sociological study, between their objectives, and finally between their results. These are reflected in differences in habitual scale of study in the two kinds of disciplines with plant geography inevitably broader. But geography is essentially a field of study, not a viewpoint in Tschulok's sense. Thus plant geography is almost incommensurable with ecology. Both flora and vegetation interest plant geographers; they investigate these entities under the viewpoints of genesis, ecology, history and distribution. Thus it seems quite impossible to re-define ecology as McMillan's "correlative geography."

Confusion is also possible when McMillan (1956: 602) equates Egler's (1942) use of the term "floristic botany" (see Table I) as the complete botany of individual plants with Mason and Stout's (1954) use of the term "plant geography." It is obvious that in Mason and Stout's usage, "plant geography," or their "comparative floristics," is not intended to cover all eight of Tschulok's viewpoints, as applied even to individual plants.

Mason and Stout have redefined plant geography in a way which takes leave of previous work on the subject. They have every right to exclude all applications of physiological data and ideas to vegetation from their consideration, but the reasons they give are certainly false. This point was considered above in presenting examples of application of Tschulok's points of view and in discussing plant competition.

The statement (Mason and Stout 1954: 249) that "the large body of literature of plant geography only rarely reports the conscious application of plant physiological research as a means of arriving at conclusions," could hardly be a stronger indictment of the plant physiological training offered to plant ecologists, including applied plant ecologists of all kinds. Fortunately the statement is incredible, as a glance at texts commonly used for plant ecology demonstrates (Braun-Blanquet 1928, 1932, 1951; Lundegardh 1954; Walter 1949-51; Daubenmire 1947; Fitting *et al.* 1954; Stocker 1952; Tansley 1954).

Mason and Stout employ the logic of causation, and plant geography is certainly one field where causation does not apply. The systems are too complex, and clear one-to-one relationships are lacking. Correlation, eventually leading to functional relationships, is suggested as a substitute. This is no new idea, but it evidently deserves re-emphasis (Hartman 1948: 120; Thieneman 1941: 315; Raup 1942: 325-6, 330-1, 345; Cain 1944: 19; Daubenmire 1947: 347; Major 1951: 392; Egler 1951: 687-8; Whittaker 1954; Westhoff 1954; Sjörs 1955). Raup quotes two of the very founders of plant geography rejecting causation as the first principle of their study. The prescience of Alexander von Humbolt and Alphonse de Candolle has been amply borne out by later work. Tansley (1920) and DuRietz (1921: 119, 123, 248) made this point near the beginning of distinguished careers. DuRietz described Hult's adherence to this view in 1881 and traced its use and misuse by other phytosociologists. Raup (1942: 337-339) quotes Livingston and Shreve as prescribing the same view, but often practicing another. Dahl's (1951: 33) logic in relating the lower altitudinal limits of certain alpine plants in Scandinavia to various functions of summer temperatures we suggest as a logical model. "Outside the [chosen] isotherm the species in question is absent or very rare, while inside the isotherm it is more or less frequent, at least in some tracts. I do not claim that the maximum summer temperature in all these cases is the direct cause of the absence of the species outside the limiting isotherm; the object is simply to draw attention to the fact that there is a parallellism between the range of the species and the isotherm in question. And the result should, of course, not be misinterpreted by saying that the species in question die when exposed to higher temperatures than that given with each species [in an appended table]."

McMillan (1956) evidently uses the term geography for the viewpoint that is usually named plant chorology. Geography, as defined by geographers, studies landscapes or regions (Berg 1947, Polynov 1946, Broek 1938, Kimble 1951, Regel 1949, Troll 1950). Therefore, it should follow that *plant* geography considers the place of plants in landscapes. Plant geography, therefore, recognizes that plants occupy area, but all bodies on the earth occupy some of its area. We do not, therefore, speak of the geography of the atoms within the space lattice of a NaCl crystal we contemplate. We may, however, investigate the geographic distribution of common salt over the earth in relation to the landscape elements. A map of common salt occurrence would not be a complete geographical study. It could be a complete chorologic study.

The plant in its landscape is a broad subject. This is plant geography. It includes the study of plants in relation to environment, and also much of the study of vegetation. It has always been floristic and vegetational. Historically there seems to be some justification for regarding plant geography as just that broad study from which arose plant ecology and chorology and much of vegetation study—a vegetation unit obviously occupying more geographic area than an individual plant. Contributions of plant geography to studies of physiology, history, genesis, and taxonomy of plants also cannot be ignored.

Both plant geography and plant ecology in their classic senses seem to have a place to fill in the study of plants. Newer, biosystematic ideas fit into the older schemes.

SUMMARY

Reference is made to McMillan's paper (1956), "The status of plant ecology and plant geography." The classical definitions of these subjects are discussed and differences between them related to scope, subject matter, and methods of study.

The position of ecology relative to other branches of science can be illuminated by Tschulok's (1910) scheme of 8 points of view applicable to any subject matter field. Ecology is one point of view; the others are composition, structure, physiology, chorology, history, genesis, and taxonomy. Each is applicable to the materials of plant geographical study, namely, individual plants and stands of vegetation. Examples of such applications are given.

In an effort at clarification, certain criticism of ecology and plant geography pertinent to the subject of this note are discussed. For example, ecology is poorly included in plant physiology because plant physiologists neither adequately analyze environments nor consider vegetation at all. Ecology has been called a potpourri of subjects borrowed from other fields, but it can better be considered a unique viewpoint which synthesizes data from other disciplines and illustrates the interdependence of scientific viewpoints. To consider ecology as studying only the distribution and abundance of plants is to ignore too much else of significance, such as quantitative variations in plant growth and plant community relationships, including the necessity of synecological data to interpret autecological data. Competition as a phenomenon illustrated in plant communities cannot usefully be neglected, since it gives point to physiological data which would describe where plants grow.

Plant geography is probably best considered as describing the place plants occupy in landscapes. Such descriptions have not usually been considered causal explanations, and they cannot usefully be considered causal.

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A COLLECTING BOTTLE FOR THE MICROBIOLOGICAL SAMPLING OF WATER

The need to collect uncontaminated water samples aseptically at any given depth for microbiological sampling has resulted in the designing of many samplers. ZoBell (1946) has summarized the problems involved and described a variety of water samplers, some of which do not ensure uncontaminated samples and others are unsuitable for depths greater than 5 to 40 meters. ZoBell's J-Z sampler probably best satisfies the needs of the microbiologist, yet some workers find it lacking, as the capillary glass tube often fails to break open. Furthermore, once the capillary tube is open there is no assurance that the sample brought up is only from the sampling level.

In connection with a microbiological project begun in 1951 on lakes in Montana, no microbiological sampler was available for use the first season (Potter and Baker, 1955). A sampling bottle consequently had to be designed that would ensure an uncontaminated sample at any point from surface to bottom and also that would stand pressures of more than 100 lbs per sq inch. This sampling device combines ease of operation at all depths and maintenance of sterility before and after sampling,

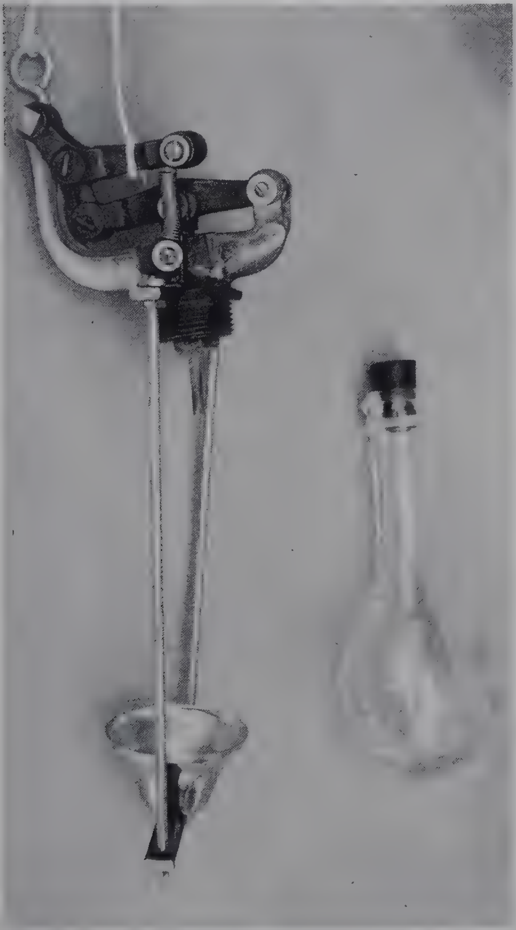

FIG. 1. Sampling bottle, unassembled and with the valve closed.

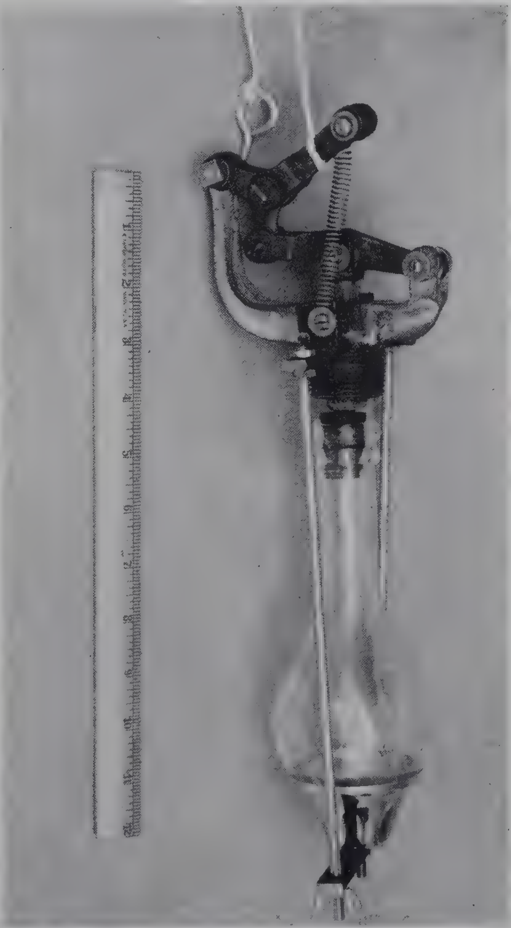

FIG. 2. Assembled bottle with valve open.

with simplicity of construction and relatively low cost of production.

The sampler is constructed from a "No-Sol-Vit" resistance glass pressure bottle with a safe working pressure of approximately 150 lbs per sq inch, of about 200 ml capacity and a compound lever trap for high pressure steam (100 lbs) from a bucket type of Armstrong steam trap (the interior mechanisms less the bucket). The bottle is standard equipment obtainable from any scientific supply house and the lever trap may be obtained from an engineering house supplying parts for steam heating systems. The traps used came from the Advance Engineering Company which has outlets in several states. Current costs for bottle and trap are about $1.50 and $10.00 respectively.

The bottle rests in a nickel plated pipe flange supported by a cross strap of brass, ⅞ x 4¾ x 1 inch, and vertical welding rods fastened to a brass angle strap (½ x ⅜ x 1 inch in vertical position and ½ x ⅜ x 1¼ inches in horizontal position) attached on the flat surface of the flange body about 1 inch above the copper inlet tube. Copper tubing of approximately 3 mm bore (inside diameter) is soldered into the seat of the valve. A one-hole, number 2 rubber stopper receives this tube when the sampler is assembled and secures the valve to the bottle. The welding rods are removable by operation of threaded ends and wing nuts, which makes a secure supporting frame for the bottle.

All parts are readily sterilized. Bottles are plugged with cotton before autoclaving. Rubber stoppers are autoclaved separately. The frame has its openings (valve and tube) plugged with cotton prior to dry sterilization in stapled paper bags. The apparatus may be assembled before departing for samples or assembled in the field. The low cost of bottles enables one to maintain a large stock. Frames may be sterilized during operations for repeated use if one employs "Roccal" and sterile water for a rinse. There is no guarantee that frames so treated are sterile, however. In the project for which this bottle was designed, the need for field sterilization has been eliminated by having enough complete sets of samplers to use one for every sample.

Cotton plugs in the valves are removed just prior to sampling. The bottle is lowered to a desired depth by means of a rope (number 6 sash cord) passed through an eye bolt on the top of the valve. An expansion spring holds the valve closed until a pull on a second or release line which is fastened between the body of the valve and operating arm, releases the tension and opens the valve. To avoid tangling of lines the release line is nylon-plastic as this slips easily and reduces to a minimum the chances of the two lines tangling. Weights may be attached to the base of the frame to reduce drifting.

By alternately opening and closing the valve, the pressure bottle fills with an adequate water sample in about 5 minutes at any selected level. Samples may be transferred aseptically to sterile flasks or containers for refrigeration and storage. A refrigerator bag with "snow gel ice" has proved satisfactory for field operations involving a span of several hours.

The illustration, Figure 1, shows the two portions of the apparatus before assembly, with the valve closed. Figure 2 shows the assembled bottle with valve open. (*N.B.* the rope was not available to the photographer.)

This water sampling bottle has operated successfully in obtaining microbiological samples of water from selected depths up to 107 meters for five summers.

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(ON THE PRINCIPLES OF GENETIC CLASSIFICATION IN BIOCENOLOGY)

Classification has always been valuable in science as a means of relating phenomena, and it usually reflects the latest advances of each field. Generally, classifications are at first based on artificial features and single concepts, later to become natural classifications founded on a synthesis of fundamental features. Classification taking into account the dynamic aspects of the subject matter are relatively advanced, and have greater practical as well as theoretical value. Only when the developmental history of an entity is considered can we understand its relationship to other entities, and develop an ability to control it. Merely the construction of a classification suggests new characteristics and properties. Any science must attempt the development of a dynamic classification as soon as it has attained sufficient maturity.

Biocenology, which has developed only during the present century, must develop a classification if it is to continue to advance. Although many ideas on classification, some purporting to be dynamic, have been published, a discussion seems in order regarding the nature of the biocenosis and what is meant by its dynamism.

The term biocenosis was first proposed by zoologists, but its usage has varied, and sometimes has implied no more than an animal aggregation—zoocenosis. It will be used here for both the animals and the plants that are found in a habitat. A question of much controversy is whether or not the natural unit should embrace environment as well as organisms, and whether or not the classification should be on this broad basis (see reviews of this question by Katsen, 1934, and Dokhman, 1937).

The cause of this controversy has been a general lack of understanding of the relationship of plants and animals to other components of the landscape, edaphic and aerial. There is at present a growing trend in geography toward recognizing such complex and integrated landscape-units.

There is a constant and complex series of transformations of matter and energy among organisms, the lower layers of atmosphere and the surface of the earth's crust. It seems appropriate to refer to the physical components of this system as a geocenosis, and to refer to the geocenosis plus its corresponding biocenosis as a geobiocenosis (Sukachev 1942). G. N. Vysotski proposed the term ecotope for the physical factors affecting a biocenosis, and Koshkarov (1938) used the word biotope for this purpose. One might consider the ecotope as comprised of a climatope and an edaphotope. In considering these complex units animals are unique in that a single individual can be an integral part of two or more biogeocenoses, as the heron which nests in the forest and feeds in the meadow.

The Leningrad group of phytocenologists uses the terms biocenosis and phytocenosis for landscape units which are essentially uniform throughout, but they might also be used in a broader sense, just as the word plant may be used for an individual organism or for a type of organism.

Just as in phytocenology equivalent stands are collectively designated as one association, equivalent landscape units can also be designated as a biogeocenosis type. One may recognize ecotope types, etc. A hierarchy, best named after the plant constituents, can be constructed by successive grouping of biocenosis types into types of biocenotic formations and types of biospheres. Although the point has not yet been clarified, landscape study and biocenology have a common meeting ground only in the biogeocenosis.

It should be clear that the biocenosis should be definable solely upon biologic features.

A natural classification of biocenoses, or their components, should be based on biologic properties which result from the coexistence of species—properties which do not reside in the individual. These attributes result in part from interference and in part from favorable interrelations, and are determined basically by (1) the ecologic character of the taxa, (2) their biologic properties (e.g., type of reproduction and growth), (3) the density of populations, and (4) the nature of the habitat. The last four must not be given a place of primary importance in biocenologic classification.

By interference above is meant the competition for light, water, and nutrients, which allows certain taxa to gain ascendency. Favorable interrelations include providing protection against sun and wind, providing fixed nitrogen, release of nutrients through decay, etc.

Our consideration of the phytocenosis must include not only the vascular plants, but bryophytes, lichens, fungi, algae and bacteria. The lower plants have complex and important roles in relation to the higher.

As a consequence of all these interrelationships a phytocenosis develops a definite structure expressing present and past conditions. A special feature of this structure is the ecologic differentiation of plants into synusiae, which collectively make up a phytocenosis just as phytocenosis and a zoocenosis make up a biocenosis. They may differ in relation to rooting depth, seasonal aspect, denseness, mode of reproduction, and litter production.

The structure and composition of the phytocenosis determines the specific manner in which it contributes to exchanges of matter and energy, the degree to which it is inimical to the implantation of addition taxa, its stability through time or direction of change, its response to disturbance, its capacity to tie up energy in organic compounds, etc. Such are community characteristics and should provide the basis for a natural classification of phytocenoses.

The characteristics of zoocenoses are expressed (1) in the form of intra- and interspecific competition, (2) in the manner by which some groups make it possible for others to live, and (3) in the manner by which certain organisms directly nourish others. Here, too, even the microscopic forms of the fauna should be taken into account in classifying zoocenoses.

The interrelationships between plants and animals are important at the biocenosis level. Here there is no direct competition, but either group may, for example, have an influence upon the other through shading. Usually the conspicuous relationship is the damage or destruction of plants by animals, but there are also beneficial influences in both directions. It often happens that the character of the phytocenosis depends on the zoocenosis. Such interrelationships must all be taken into account in defining the biocenosis.

The basic unit of classification is the biogeocenosis, which consists of one type of photocenosis (plant association) and zoocenosis that always occur together and have uniform characteristics wherever found. As these units are compounded at successive levels in a hierarchy there are fewer and fewer common characteristics at higher levels. The choice of features used in grouping determines the naturalness of the classification.

The question arises, should dynamics be given an important place in a natural classification. According to dialectics, development proper consists of changes brought about through internal conflicts—through competition. There is no biocenosis where organisms are so scattered that competition does not occur.

The term development is used for changes in the community that are related to the progress of the season. It is also used for the events that take place after a pine forest is logged. In the latter case there is no development of vegetation,—just a maturation of young plants which alters environment and species interrelations, which hardly involves inner conflicts.

Primary succession is a very different phenomenon. The process of developing the climax is development in the present sense of the word. There is exchange of matter and energy between organism and environment, and the organisms multiply and spread, all of which involves competition. The phytocenosis plays the leading role in this. I have elaborated on these matters previously (1942).

It should be noted that succession, or syngenetics as I proposed to call it some time ago, has been studied mostly from the plant standpoint. Even less attention has been given the development of biocenoses through time, which has been related to the evolution of taxa. I first pointed out this phase of study in 1915, and in 1942 called it phytocenogenesis. Plant synecologists are becoming interested in this, but little is as yet published on it. Laemmermayer (1923) has considered the antiquity of *Fagus* associations and Lippmaa (1938) has discussed the origin of one of the synusiae of broadleaved forests, which he considers independent phytocenotic units (unions). More recently Leskov (1943) has dealt with principles of vegetation classification considering the origin of Caucasian *Abies* forests, and Tolmachev (1943) has studied the origin of taiga. Prokhorov and Morozov much earlier have discussed a genetic classification of *Quercus* forests in the sense of origin attributable to edaphic factors. But this was not properly a syngenetic, but rather simply an ecologic classification.

Leskov's principles are worth exploring. His main thesis is that the association has an evolution parallel to that of its influent species, consequently the latter are the best indicators of historic relationships which must be worked out as the first step in evolving a natural classification. This premise led him to try to construct a system based on influents and dominants of varying degrees. His lower units were related by considering the composition of influents and dominants, the structure of the phytocenosis, the sociologic and ecologic similarities among associations, and the taxonomic relations of the influents. At higher levels he also considers taxonomic relations as useful indicators of ecological and synecologic relations.

Let us see how these principles apply to vegetation other than *Abies* forests. Accordingly we must assume that all Pinus-dominated forests are more closely related to each other than any is related to any Larix-dominated forest. But this is not true. The Pinetum vacciniosum is much closer in composition, structure, and ecology to the Laricetum vacciniosum than to the Pinetum tiliosum, P. quercetosum, etc. The same holds for the P. sphagnosum and L. sphagnosum. These twinned associations vitiate Leskov's principle of linking phylogeny of the dominant layer with the ecology of associations.

Let us further compare the Pinetum tiliosum, with herbaceous undergrowth, to the P. cladinosum, with lichen-dominated undergrowth. The former is historically related to the steppe and the latter to tundra. Both could not be considered as having their evolution shaped by the dominant *Pinus*.

Both *Pinus* and *Larix* are such weak influents that the undergrowth developed independently. The herbaceous undergrowth is related to conditions created by the *Tilia* rather than the *Pinus*, and probably segregated out in Tertiary Time. In the Pinetum oxalidosum, *Oxalis acetosella* is dependent upon influences created by the mossy carpet. Thus the *Tilia* and moss are more influential than the *Pinus*. Although Leskov thinks physiognomy should not figure in classification, his method actually produces units with more physiognomic than ecologic, sociologic, or paleoecologic uniformity. In general *Pinus* forests have not differentiated out of one primitive stock, but through the *Pinus* encountering and mixing with different floristic elements. The *Pinus* has broad ecologic amplitude and occupied territory favorable to diverse kinds of undergrowth. To be sure the *Pinus* exerted some influence by shading, using soil moisture, casting litter, etc. Basically however the community arose out of the competitive relations of the plants which allowed *Pinus* and the others to grow together under certain climatic and soil conditions.

In view of Leskov's idea that associated plants have similar paleoecologic histories let us consider the Pinetum oxalidosum in which the following serve as co-dominants: *Asarum europaeum, Asperula odorata, Maianthemum bifolium, Trientalis europaeum, Lycopodium annotinum, Vaccinium myrtillus, Pyrola secunda, Linnaea borealis,* etc. According to Lippmaa the first four of these developed during Tertiary time under deciduous forests where shade was intense in summer and a delicate type of leaf litter; the rest of the plants undoubtedly are related to coniferous forests. Thus even in this one association the herbaceous dominants have had different origins.

Leskov also claimed that all associations dominated by one species or species-complex must be grouped separately from these dominated by another species or species-complex. Therefore the Piceeta excelsae and P. obovatae on the one hand, and the Lariceta sibiricae and L. dahuricae, on the other, belong to different groups, although all are extremely close in structure and ecology.

It is interesting to compare associations dominated by *Larix sibirica* with *L. decidua* on the one hand, and *L. sibirica* with *L. dahurica* on the other. The first two species are very closely related phylogenetically but not ecologically. Their herbaceous undergrowth is quite different. In contrast *L. dahurica* and *L. sibirica* are less closely related phylogenetically but their undergrowth is more similar than between *L. subirica* and *L. europaca*.

According to Leskov *Picea-Betula* forests of the N. Hemisphere must belong to the same formation although all they have in common is an Arcto-Tertiary ancestral type, whereas forests of *Fagus* and of *Northofagus,* or deserts dominated by *Cactaceae* and by *Euphorbiaceae* must belong to different formations, even though their structure and ecology are very close.

These difficulties with Leskov's principles as applied to climaxes become magnified when seral communities are classified.

Thus Leskov's principles are unsatisfactory. Just as the system of Prokhorov and Morozov developed in the first decade of this century as a result of attention to Dokuchaev's ideas concerning soils, recent paleo-botanical work stimulated phytocenology. This work showed that there is no close relationship between the genesis of species and of associations. The explanation seems to be that evolutionary convergence in structure and in ecology may take place at either the species or the association level. Concepts related to species and individuals cannot be applied directly to associations. One must not forget that in biocenoses there is no reproduction similar to that of organisms. Phylogeny and ontogeny are related in individuals but there is nothing analogous at the phytocenosis level.

The transferance of ideas from the field of idiobiology to community study may easily lead to incorrect conclusions. For example, Leskov writes that we can assume that the primeval stock for European-Mediterranean forests was an Arcto-Tertiary mixed forest. Here evolved the sociologic properties of the influents and to these were added the ancient herb synusiae that today are so characteristic throughout. By elimination of certain woody components our existing communities came into existence.

This concept, borrowed from Sinska smatters after Turesson and other geneticists who believe that species evolve by genetic differentiation. It is doubtful if the present forests represent divergence from a single rich Tertiary type, but rather there must have been different kinds of forest then, so that different modern forests had different Tertiary ancestors.

In all classifications the authors have paid much attention to dominants of great vigor which were influential in determining the character of the phytocenoses. Yet all species are not critically affected by the conditions imposed by these influents.

The crux of the situation seems to be whether one phytocenosis can have different origins. In some cases the interrelationship among species evolves slowly as the phytocenosis develops through time. In others species evolved in separate phytocenoses come together, like Asarum and Asperula which have invaded certain of the Picea forests although they are believed to have evolved in the Tertiary broadleaved forest. Both processes may take place simultaneously, or the second may change into the first.

Where there are dominants that exert strong influences there still may be a large proportion of species, including codominants, that had origins in other phytocenoses. And where dominants do not superimpose highly specialized influences on the habitat all the flora may have had diverse origins. Therefore Leskov's principles are faulty. If they do not hold for forests where the dominant (e.g., *Abies nordmanniana*) has a strong and specialized influence, they certainly will not hold for associations with less unusual biotic environment, which is usually the situation.

If we abandon Leskov's basis of emphasis on floristic derivation, and consider as bases only those things which express the essence of a phytocenosis, a classification emerges which cuts across the units based on similar derivation. This principle applies to zoocenoses and biocenoses as well as phytocenoses.

The following types of origin can be distinguished:

Cenogenesis—the development of associations through geologic time in part by convergence of elements (selectogenesis) and in part by slow evolution (phylocenogenesis).

Syngenesis—successional derivation which represents a much more rapid type of development.

Although these processes are closely related to climate and soil, they have distinctive attributes which enable them to be studied separately.

As pointed out earlier, a natural classification of phytocenoses must rest upon features which are involved in transformations of matter and energy in the biogeocenosis as determined by the synusiae involved. Since these processes are also involved in succession there should be complete agreement in classification from both viewpoints. But we have little information on successional processes and these mostly from just the plant standpoint. This is one of the most important problems in biocenology.

A classification based on development and the resultant complexity of sociologic structure, is not harmonious with one founded on cenogenesis for those which have similar derivations may differ considerably in complexity and efficiency in use of matter and energy. Both classifications converge at the association level but diverge higher in the hierarchy. Both have great theoretical value in putting facts into perspective and suggesting new approaches and new viewpoints, but the development of a natural successional classification of biocenoses is important for the development of biocenology.

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GERMINATION AND SEEDLING ROOT GROWTH OF *BOTHRIOCHLOA AMBIGUA* IN RELATION TO INVASION OF NATIVE PASTURE

Introduction

Moore (1957) has pointed out that on the Southern Tablelands and Southwestern Slopes of New South Wales *Bothriochloa ambigua* S. T. Blake has become an important constituent of the native pastures, and showed that following invasion significant changes occur in certain soil characters. Current investigations are aimed at obtaining information which will enable an understanding of the ability of *B. ambigua* to compete successfully with the *Danthonia* species which it replaces.

This paper deals first with the effects of temperature, soil moisture and depth of sowing on the germination of *B. ambigua*. A similar investigation was reported by Moore (1946) for *Danthonia caespitosa* Gaud in Freycinet, under the name *D. semiannularis*. It is clear from the revision of the genus by Vickery (1956) that the species concerned in this work was *D. caespitosa*, not *D. semiannularis*. In addition, a study of seedling root growth in *Bothriochloa* and *Danthonia* is reported. Differences in initial root growth could significantly affect competition between species, and so determine which one would ultimately colonize an area. The author is particularly indebted to Dr. L. A. T. Ballard, C.S.I.R.O., Canberra, for his suggestions leading to the design of the apparatus used for the root-growth studies.

Methods

The *Danthonia* seed used was a mixture of *Danthonia carphoides* F. Muell. ex. Benth., *D. auriculata* J. M. Black and *D. pilosa* R. Br. as collected in the field. No attempt was made to select only one species because in the field *B. ambigua* is competing with a mixture of all three. The *Danthonia* seed and the *Bothriochloa* seed were treated in the hammer mill to separate the caryopses.

Germination

Temperature.—Seeds were geminated on filter paper in Petri dishes, with the addition of 5 ml water to each dish. Three dishes, each containing 100 seeds, were maintained at each temperature, 10°C, 20°C, 25°C, 30°C, and 35°C. Daily counts were made of germinated seed.

Soil moisture and depth of sowing.—The technique used to study the effect of soil moisture and depth of sowing was essentially that described by Moore (1946). The only modifications were that soil moisture levels were based on moisture equivalent (M.E.) instead of field capacity, and an additional treatment at a moisture level maintained at 2 M.E. was included. This was considered desirable because it appears that *B. ambigua* spreads rapidly during seasons of exceptionally high rainfall when the soil may be saturated or near saturated for relatively long periods. The moisture equivalent was determined by the method described by Piper (1942). The soil used was a gray-brown sandy loam from Black Mountain, A.C.T., of moisture equivalent 11.6 per cent.

The soil moisture levels used were:

1. The soil moisture was maintained as near as possible at 2 M.E.
2. The soil moisture was maintained as near as possible at M.E.
3. The moisture content of the soil was brought to M.E., then allowed to dry to 60 per cent M.E. before water was added to bring the moisture level back to M.E.
4. As for treatment 3, except that the moisture level was allowed to fall to 40 per cent M.E. before water was added.

The soil trays for treatments 1 and 2 were placed on cotton wool and covered with bell jars to prevent rapid evaporation, as otherwise the moisture levels could not have been kept near the required values. All trays were weighed twice daily and water added as required.

Seed was sown on the surface of the soil, and at depths of 0.25 inch and 0.5 inch, 100 seeds being sown in each tray in 10 rows of 10 seeds each. Three trays were used for each combination of moisture level and depth of sowing.

Room temperature during this experiment was approximately 20°C.

Seedling root growth

The apparatus used for the measurement of root elongation consists of a Perspex tank (Fig. 1) 10″ x 12″ x 7″ with Perspex pegs set into the top and bottom of the walls at distances such that ten Perspex plates are held at an angle of 70° to the horizontal.

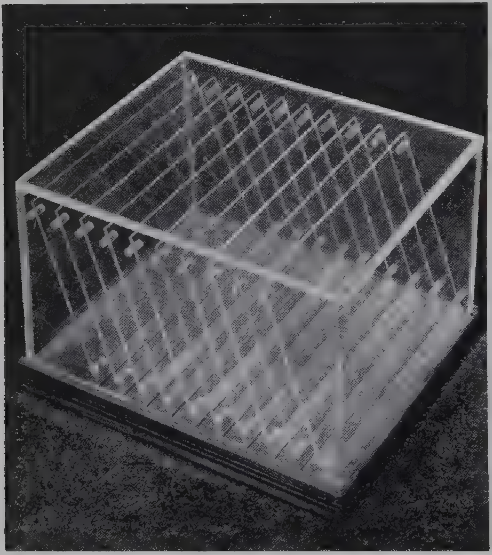

FIG. 1. Apparatus used for studying seedling root growth. The plates have been reversed to avoid use of the rebate, which can be seen at the bottom of each plate.

This angle of 70° was chosen because it allows of vertical growth of the shoot, the seeds are readily retained on moist filter paper, and, with few exceptions, the roots grow straight downwards on the surface of the filter paper. Originally it was thought desirable to provide a rebate of 0.5 inch width at the top of the plates to support the seeds. However, initial trials indicated that the seeds should be placed more than 0.5 inch from the top of the plates, and that growth of the root on the surface of the filter paper was more likely to occur if the seeds were placed on a flat surface. Possibly for use with large round seeds, a suitable rebate in the plate would be useful.

The tank is approximately half-filled with water, and the Perspex plates covered with moist filter paper. Seeds of the species to be tested are placed on the plates about one inch from the top, care being taken to place them in such a manner that the radicle is pointing downwards. The tank is covered with a Perspex lid to maintain high humidity and moist paper at the position of the seeds. On germination the radicle normally grows straight, and remains in close contact with the filter paper. Should the radicle grow away from the filter paper, it is advisable to adjust the placing of the seed, as otherwise the root tip will wither and die. If desired, the tank can be protected from light. The plates are readily removed from the tank for measurement of root lengths with dividers and ruler.

Five plates were used for each species, with 16 seeds on each plate. Root lengths to the nearest mm. were measured at 9 a.m. daily.

RESULTS

Germination

Effect of temperature.—Daily counts of germinated seed at the five temperatures used are shown in Figure 2. The fact that total germination at 30°C is lower than that at 20°C, 25°C and 35°C is difficult to explain, unless the sample of seed used at this temperature contained an abnormally high proportion of non-viable seed. Shortage of seed and the impracticability of obtaining a fresh supply made it impossible to repeat the trial. It would appear, however, that the important influence of temperature within the range 20°C to 35°C is in its effect on the rate of germination in the early stages and on the rate of growth of the seedlings.

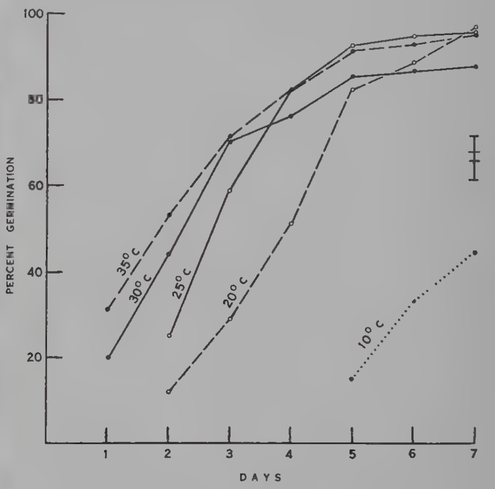

FIG. 2. Effect of temperature on germination of *B. ambigua.* Minimum differences for significance at the 5 per cent, 1 per cent and 0.1 per cent levels are shown for total germination.

Soil moisture and depth of sowing.—Figure 3 shows the effect of soil moisture at each of the three depths of sowing on the germination of *B. ambigua.* When the seed is sown on the surface, total germination at 2 M.E. and M.E. is significantly greater than at 60 per cent M.E. and 40 per cent M.E., while germination at 60 per cent M.E. is greater than that at 40 per cent M.E. When the seed is sown at 0.25 and 0.5 inch depths, total germination is similar for the three highest moisture levels (though at 0.5 inch germination at 2 M.E. is greater than that at 60 per cent M.E.), but is significantly lower at 40 per cent M.E. At all sowing depths the rate of germination is greatest at 2 M.E.

Figure 4 shows the effect of depth of sowing at the

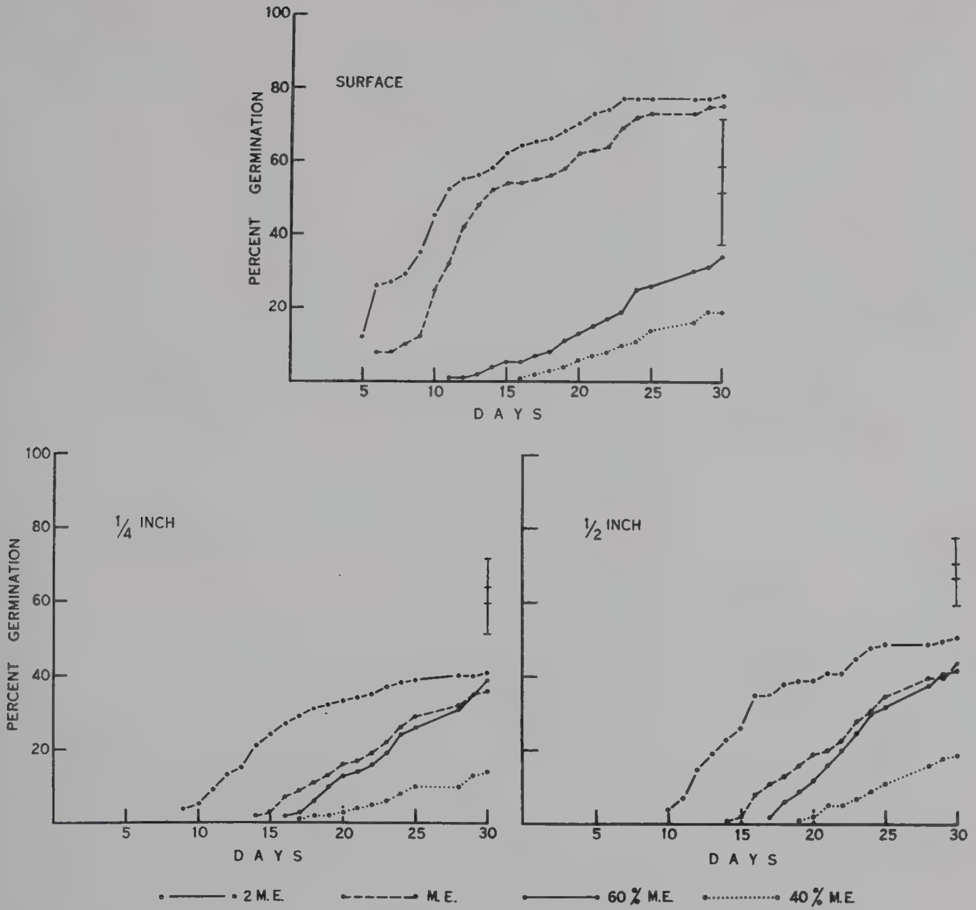

Fig. 3. Effect of soil moisture at three depths of sowing on germination of *B. ambigua*. Minimum differences for significance at the 5 per cent, 1 per cent and 0.1 per cent levels are shown for total germination.

four moisture levels used. At both 2 M.E. and M.E. germination of surface sown seed is markedly superior to that of buried seed. At these moisture levels germination of seed sown at 0.5 inch is greater than that sown at 0.25 inch. At 60 per cent M.E. and 40 per cent M.E. depth of sowing has little influence on germination.

Seedling root growth

Figure 5 shows the mean daily root lengths of *B. ambigua* and *Danthonia*. It is clear that the rate of seedling root growth of *B. ambigua* is greater than that of *Danthonia*.

Discussion

On the Southern Tablelands and Southwestern Slopes of New South Wales, temperature and soil moisture conditions are most likely to be favorable for germination of both *B. ambigua* and *Danthonia* spp. in autumn and spring. It would appear from the data presented that *B. ambigua* will germinate over a wide range of temperatures, but that the optimum temperature is in the neighbourhood of 30-35°C. Cashmore (1932) reports that the optimum temperature for germination of *Danthonia* spp. is 18-20°C.

Germination of *B. ambigua* is favoured by high soil moisture levels, but even under conditions of periodic drying to 40 per cent M.E., germination may still be about 20 per cent at 0.5 inch sowing depth. Germination of *Danthonia* seed at low soil moisture levels may be less than 10 per cent with surface sowing, while seed buried to a depth of 0.5 inch does not germinate (Moore 1946). Both grasses behave similarly under conditions of continued high moisture supply and shallow sowing, but as moisture is reduced and depth of sowing increased, *B. ambigua* is the more likely to be successful.

The results suggest that, under conditions of favourable soil moisture, germination and establishment may be largely influenced by temperature. In autumn and spring, when temperatures are relatively low, *Danthonia* spp. may be expected to establish more successfully than *B. ambigua*, while the latter would be favored during the summer. This is consistent with the observation that invasion of native pasture by *B. ambigua* seems to occur chiefly during exceptionally wet summers.

B. ambigua often rapidly becomes the dominant species on silt deposits washed from higher levels during heavy rain (Moore 1957). This is probably related to

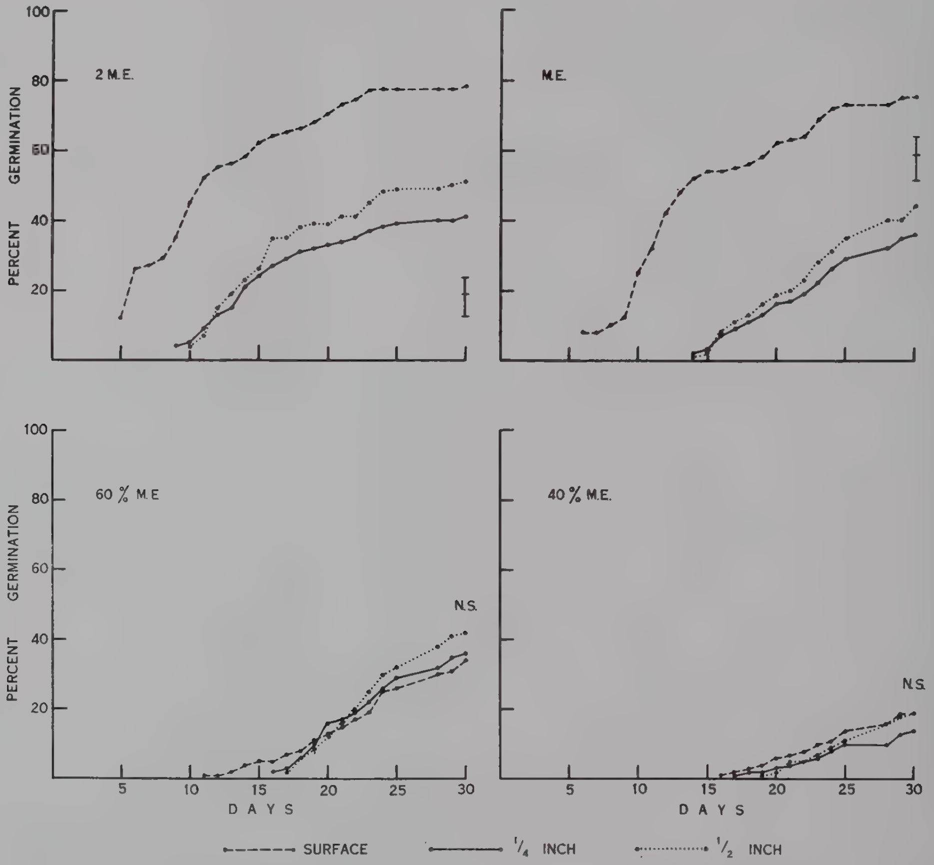

FIG. 4. Effect of depth of sowing at four soil moisture levels on germination of *B. ambigua.* Minimum differences for significance at the 5 per cent and 1 per cent levels are shown for total germination.

the greater ability of this grass to establish from buried seed as compared with *Danthonia.*

The significance of initial root growth in relation to the survival of seedlings has been demonstrated by previous workers for a variety of plants. Blake (1935) made a detailed study of a number of prairie plants. She found that following germination they rapidly develop a deeply penetrating root, and considered that this was "a major adjustment to the prairie environment" in that it enables newly established seedlings to survive a period of surface drying of the soil. Plummer (1943), in a study of twelve range grasses, concluded that "total root development prior to summer drought appears to be directly associated with success." He considered that depth of penetration in the earlier stages is of less significance than total root development. No indication is given of the likelihood of surface drying during the early seedling stage, and it is presumed therefore that the roots of the grasses he examined could keep ahead of surface drying of the soil. Plummer also demonstrated that the results of glasshouse studies of root development correlated well with success or failure in the field.

During autumn and spring, when conditions are most likely to be favorable for germination, rapid drying of the surface soil frequently follows beneficial rain. If a seedling is to become established, root penetration must keep in advance of the dry layer of soil.

The more rapid development of the primary root of *B. ambigua* as compared with that of *Danthonia* spp. gives the former an initial advantage when growing in competition with the latter. Under drying conditions *B. ambigua* seedlings would be more likely to survive than *Danthonia* seedlings. When the soil moisture remains at a high level for a long period, such as during seasons of exceptionally high rainfall, germination of both grasses is likely to be satisfactory, but again the more rapid root growth of *B. ambigua* gives it an initial advantage in competition with *Danthonia.* A study of competition between the two grasses has been commenced by the author, and it is already clear that the growth of *B. ambigua* seedlings is little affected by competition with *Danthonia* seedlings established at the same time, suggesting that the more vigorous root growth in the early seedling stage of *B. ambigua* continues in the subsequent stages. Details of this work will be published at a later date.

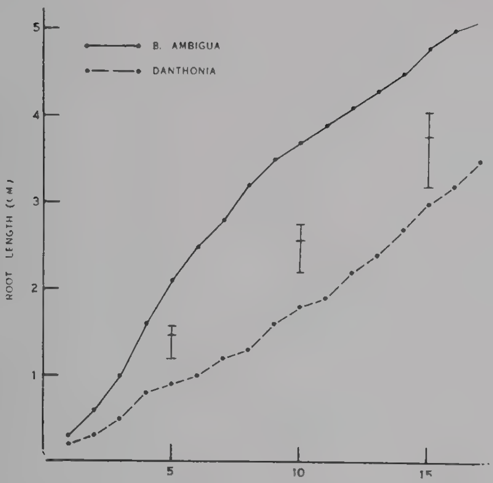

FIG. 5. Mean daily root lengths of *B. ambigua* and *Danthonia* seedlings. Minimum differences for significance at the 5 per cent and 1 per cent levels are shown at 5, 10 and 15 days.

SUMMARY

The effect of temperature on the germination of *B. ambigua* was determined at 10°C, 20°C, 25°C, 30°C, and 35°C. Over the range 20°C to 35°C the most important effect of temperature is probably its effect on rate of germination and seedling growth.

The combined effect of soil moisture and sowing depth was examined using the technique previously applied to *Danthonia* (Moore 1946). Significant effects of both soil moisture and sowing depth have been demonstrated. The results are discussed in relation to the earlier work with *Danthonia*, and to field establishment.

Measurements of root length of *B. ambigua* and *Danthonia* seedlings showed that the roots of *B. ambigua* grew more rapidly than did those of *Danthonia*.

It is suggested that the more rapid development of the root of *B. ambigua* gives this species a distinct advantage in seedling competition with *Danthonia*.

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THE EFFECTS OF COMPLETE INUNDATION UPON SEEDLINGS OF SIX BOTTOMLAND TREE SPECIES[1]

Studies of regeneration and succession of bottomland hardwood trees often emphasize the effect of flooding upon regeneration. However, few tests have been made to determine the relative tolerance to complete inundation of the various bottomland hardwood species.

The following study was set up to test the effect of complete submergence upon survival, for different periods of time, of the following bottomland species: silver maple (*Acer saccharinum* L.), eastern cottonwood (*Populus deltoides* Bartr.), boxelder (*Acer negundo* L.), black willow (*Salix nigra* Marsh.), green ash (*Fraxinus pennsylvanica* Marsh.), and redgum (*Liquidambar styraciflua* L.). These names follow Little (1953).

Previous observations concerning complete submergence are almost nil, but it seems to be a well-accepted fact among biologists that trees will stand but short periods of complete submergence during the growing season. Putnam (1951), in discussing the floodplain forests of the Mississippi River, stated, "A few days submergence while the tree is in leaf is fatal." He also stated in the same publication that, "Only willow survives complete inundation during the growing season." Demaree (1932), in experiments with cypress seedlings submerged in Reelfoot Lake and the Lower St. Francis River, found all plants dead after two weeks of submergence. Brink (1954), based on observations in the lower Fraser River Valley, stated that, "Cold, swift water did little but delay the growth of most (Western) species; slow moving, or stagnant, warm water, on the other hand, caused the death of nearly all aerial vegetation after a day or two of flood." Boxelder was one of the species observed.

Floods in southern Illinois during the early part of the growing season are a common occurrence. Fifteen year records (1939-1954) taken by the Illinois State Water Survey at the Murphysboro gauging station along the Big Muddy River showed that the river failed to reach flood stage in only two years. Flooding was most frequent during the month of May. The average consecutive time the river was out of its banks was 17 days. Differences in flooding tolerances doubtless have considerable bearing on the species occurring in bottomlands through selective killing effect upon reproduction.

[1] Originally submitted as part of completed doctoral dissertation at the State University of New York College of Forestry at Syracuse University.

TABLE I. Results of complete submergence for varying periods of time of six species of bottomland hardwoods

	LENGTH OF COMPLETE SUBMERGENCE IN DAYS				
Species	2	4	8	16	32
Cottonwood	Dead areas appeared both lower and upper leaves; recovered quickly.	Large dead areas on all leaves; recovered quickly; new leaves appeared within a few days.	All lived; lower leaves lost on all plants; recovered slowly.	All died soon after removal.	All died.
Willow	No apparent effect.	Lost a few lower leaves; recovered quickly; new leaves appeared within a few days.	All lived; all lost some lower leaves; slightly chlorotic; recovered quickly.	All lived; leaves slight to very chlorotic; several lower leaves dropped off; all recovered quickly.	Appeared very chlorotic; all but upper 3-4 leaves dead; recovered quickly and grew well.
Redgum	2 trees showed dead areas on leaf margins; recovered quickly.	All trees showed dead areas; mostly on lower leaves; recovered slowly; new leaves appeared within 8 days.	All lived; slightly chlorotic; recovered slowly.	2 lived; 1 died; only small dead areas on leaves live trees; recovered slowly.	All died.
Ash	No apparent effect.	No apparent effect; new growth appeared within a few days.	All lived; good color; lost some lower leaves; recovered quickly.	All lived, good color upon removal; wilted slightly but recovered quickly.	All died.
Boxelder	No apparent effect.	All slightly chlorotic; recovered slowly; two trees produced new leaves within 9 days.	All lived; moderately chlorotic; terminal leader died on two trees; recovered slowly.	2 died; 1 lived; terminal leader died on 1 living tree, recovered slowly.	All died.
Silver Maple	Wilting of lower leaves; recovered slowly.	All died.	All died.	All died.	All died.

PROCEDURES

Except for silver maple, which was grown from seeds sowed in vermiculite in a greenhouse, wildlings of current year seedlings were collected in the field. Both the wildlings and the greenhouse grown plants were transplanted into 2½ inch pots containing a prepared loam soil. The seedlings were allowed to grow in the pots for three weeks to offset possible transplating injuries. After three weeks of growth in the pots, vigorous seedlings of uniform appearance were selected for the inundation study. All species except soft maple appeared thrifty at the start of the test.

A test was made of the ability of the six species to withstand complete inundation for periods of 2, 4, 8, 16, and 32 days. Three tanks that could be filled to a depth of 20 inches of water were used, each tank representing one replication for a total of three replications. Assignment to a tank and a position within a tank was done in a random manner. Throughout the test the tanks were filled and kept filled with water from an adjacent pond. The seedlings were approximately 3 inches high when the test began. They were kept inundated with approximately one foot of water. The water was reasonably free of suspended material although some alge were present. All the seedlings were placed in the tanks at the same time. One seedling represented each treatment in each replication. Thus, a total of three seedlings, one in each replication, was subjected to each period of submergence.

The tanks were placed outdoors in an area exposed to full sunlight in the morning but shaded after approximately 2:00 p.m. The temperature of the water in the tanks at the plant level, based upon measurements made at 8:00 a.m. and 4:00 p.m. on several different occasions, ranged from 88° to 93° F.

As the seedlings were removed from the tank after the appropriate time interval, they were placed outdoors under partial shade. The test began July 8 and ended August 7, 1954.

RESULTS

The results of the study are shown in Table I. All species except silver maple survived 8 days of complete inundation. After 16 days all replications of willow and ash survived; two out of the three gum survived; one of the three boxelder survived, but none of the cottonwood or silver maple survived. After 32 days submergence only willow survived. Survival was based upon death of both tops and roots. There was no subsequent sprouting from the roots of any of the trees with dead shoots.

The recovery rate of the surviving trees also varied among species. The surviving willow and ash recovered quickly in all cases. The surviving cottonwood, redgum, and boxelder trees recovered more slowly than the ash or willow from the effects of submergence beyond the 4 day period; whereas silver maple seedlings subjected to but 2 days inundation recovered more slowly than any of the other species.

The six species, ranked according to their relative tolerances to complete inundation, were as follows: willow, green ash, redgum, boxelder, cottonwood and silver maple.

Discussion

Many factors such as temperature, amount of water movement, chemicals and organic matter in water, microbes, algae growth and the like, would be expected to affect the length of time that seedlings will withstand complete submergence. In the test described above the water movement was nil and the temperatures remained high throughout the entire period. Thus it is interesting to note that all seedlings except silver maple survived 8 days of inundation; some seedlings of ash, redgum and boxelder survived 16 days of inundation and the willows survived 32 days of submergence. The maple did not appear thrifty at the beginning of the study so it is possible that the initial low vigor may have contributed to their poor survival; however, all the other species were vigorous, healthy-looking seedlings.

In general the relative tolerances to flooding brought out by this test correspond to the sites on which the species are found under field conditions. Hosner (1957), based upon an extensive survey of reproduction in the bottomlands of southern Illinois, indicated that of the six species in the above test only ash, redgum and willow reproduction could be expected to survive in poorly-drained areas subject to prolonged inundation.

If the same effects carry through with older trees, the results of this study also seem to partially explain the presence of poorly-formed boxelder and other small trees that have often been noted in bottomland areas subjected to flooding. The dieback of the terminal leader of many of the submerged seedlings suggests that perhaps some of this injury and resultant poor form is caused by prolonged submergence.

Conclusions

This study suggests that floods in bottomland hardwood areas during the growing season exercise a selective effect upon the species of tree seedlings surviving. Under conditions similar to those in this study it seems that only willow seedlings can survive 32 or more days of complete inundation. Where complete submergence occurs for half that period, many ash, some redgum and possibly a few boxelder can survive. Cottonwood and silver maple seedlings survive only with less than 16 days inundation.

The rate of recovery of the surviving trees also varies. In general, the willow and ash recovered quickly whereas the others showed the effects of submergence for longer periods of time.

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HIGHER PHOSPHATE VALUES IN SOILS UNDER TREES THAN IN SOILS UNDER GRASS

The water-soluble phosphate values in the soil are higher in the tree-covered land than in similarly situated grassland in one transect of soil samples in California. Frank Harradine and Hans Jenny collected the soil samples which are listed in Harradine's (1954) unpublished doctoral dissertation. The phosphate analyses of these samples were carried out in the Soils Laboratory in the University of California. The significance of the phosphate values in this tree-grass dichotomy went unnoticed until I examined them.

The sites were from a transect extending up the foothills to the crest of the Sierra Nevada in Fresno County, California. For their purposes they sampled sites that were comparable in slope (16-28°), aspect (S.E. & E.), age (mature), parent material (granodiorite), and organisms (no barrier to seed movement present). For any given location three samples were taken; these had the same climate. Over the transect as a whole, climate was the variable that was of primary interest. The change in elevation provided the basis of the change in climate. I utilized only the lower portion of the transect. At the lower elevations three samples of soil were taken at each site. One sample was taken under each of the following vegetation types where this was possible: oaks (black oak, *Quercus kellogii;* blue oak, *Q. douglasii* or live oak, *Q. wislizenii*), pines (digger pine, *Pinus sabiniana* or ponderosa pine, *P. ponderosa*) and grass (*Bromus, Festuca* and *Avena*).

The portion of the transect selected for my phosphate study begins at 750 feet at the San Joaquin Range and Experiment Station and extends to the Beal River and Highway 168 at an elevation of 4100 feet. No evidence of cattle droppings, trailing, etc., were observed on seven of the thirteen sites in this portion of the transect. Three sites had evidence of cattle and at the three other sites no samples of soils under grass were taken. The seven comparable sites without evidence of cattle were used in this study (Table I). At one of the seven sites there were only grass and oak; on the remaining six sites the soil was sampled under grass, pine and oak.

Harradine found that organic carbon and organic nitrogen as well as the ratio between these two were a function of climate. No correlation was present, however, between phosphate content of the soil and elevation; therefore, no correlation of phosphate with climate appears warranted. The climatic variable (average air temperature, 52-61°F. and average precipitation 15-34 inches) is considered to be effectively constant. Even when a ratio of phosphate value to moisture equivalent is made to re-

TABLE I. Phosphate values in the soil solution in ppm. phosphate for soils under grass and trees in a transect in the lower Sierra Nevada, Fresno County, California

Elevation	Ppm. PO_4 under grass	Ppm. PO_4 under pines	Ppm. PO_4 under oaks
750	.64	....	.90
1,200	.40	.50	1.06
1,750	.22	.40	1.12
2,050	.28	.62	.44
2,200	.28	.58	.62
2,700	.40	1.08	.52
4,100	.40	.48	1.70

TABLE II. Statistical analysis of the phosphate values given in Table I for the comparison of those values under grass and oak and under grass and pine

Vegetation compared	Mean difference of paired observations	Standard Deviation	Standard error of the mean	"t"	Number of observations	Significance level
Grass and oak (mainly blue oak one live oak and one black oak)	.549	.434	.164	3.35	7	.015
Grass and pine (digger pine and one under ponderosa)	.280	.222	.0906	2.8	6	.04

move soil texture as a factor in the water relations of the soil no correlation between phosphate values and climate is discernible. The main variable, then, is plant cover—grass, pine or oak.

Statistical calculations were made by me of the difference between the phosphate levels of paired observations. Two sided "t" tests of the significance of paired differences as compared to zero were made, e.g., the phosphate value under grass was subtracted from the phosphate value under oak at each site. If on the average no difference existed between the phosphate levels under grass and oaks or grass and pines then the sum of the differences of paired values would be zero or very small. Here, on the contrary, the "t" test indicated that the phosphate levels are significantly higher under oaks than under grass (.015 level) and under pines than under grass (.04 level) (Table II).

The mechanism suggested to account for this observed difference is the differential phosphate turnover by the two types of plants. Because of the deeper root penetration and longer active growth period of the trees, as compared to the grasses, it is suggested that the trees produce more organic material and as a result bring up more phosphate. This is in part substantiated by Harradine's findings that the organic nitrogen and organic carbon content of the soils under trees tended to be higher than under grass.

Further studies of the phenomenon are suggested to determine the effects of parent material, climate and slope on the amount of phosphate in the soil.

SUMMARY

The soil solution phosphate is higher in soils under a tree cover than a grass cover when the other soil forming factors have been kept relatively constant. The transect of soil samples for this study was made in the foothills of the Sierra Nevada in Fresno County, California. The statistical "t" test indicated that the phosphate levels are significantly higher under oak trees than under grass and similarly under pine than under grass.

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STUDIES OF PLANKTON CENTRIFUGE EFFICIENCY[1]

The use of a continuous centrifuge such as the Foerst Electrical Centrifuge is a standard technique in quantitative studies of plankton populations (Juday 1926; Welch 1948; American Public Health Association 1955). Studies of the summer plankton communities of Pymatuning Reservoir begun several years ago have indicated that use of the Foerst centrifuge in the manner recommended by the manufacturer and by standard books on limnological methods (6 to 8 minutes per liter of water) did not remove more than about half of the suspended organic material from the waters of this highly productive body of water during the height of the summer bloom. Some attention has been given to this problem in an attempt to measure the effectiveness of the standard plankton centrifuge on plankton communities of Pymatuning Reservoir and to determine a procedure for more effective use of this instrument in the study of waters supporting high plankton populations.

Initial studies on the removal of suspended materials from Pymatuning Reservoir by centrifugation were made by observing changes in light absorptive capacity before and after consecutive centrifuge runs. Readings of light absorption by lake water were made with a Klett-Summerson colorimeter filter with a red filter (maximum transmission peak at 660 millimicrons). The water was then run through a Foerst Electrical Centrifuge, at the rate of 7 to 8 minutes per liter, three successive times as a continuous centrifuge operation. Stopping the centrifuge between successive runs without removing the centrifuged material resulted in irregularities in results since material was thrown out of the cup when the motor was started again. Colorimeter readings were taken on the water after each centrifugation. Typical data from water collected at different seasons of the year are presented in the accompanying graphs of Figure 1. It can be seen that during the height of the summer bloom, on July 28, 1952, a single run of 6 to 8 minutes through the centrifuge reduced the scale reading less than two thirds, from 29 to 10. A second centrifuging for the same length of time reduced the reading to four. A third run reduced the value to three. An additional run did not lower

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[1] Pymatuning Laboratory Publication No. 17.

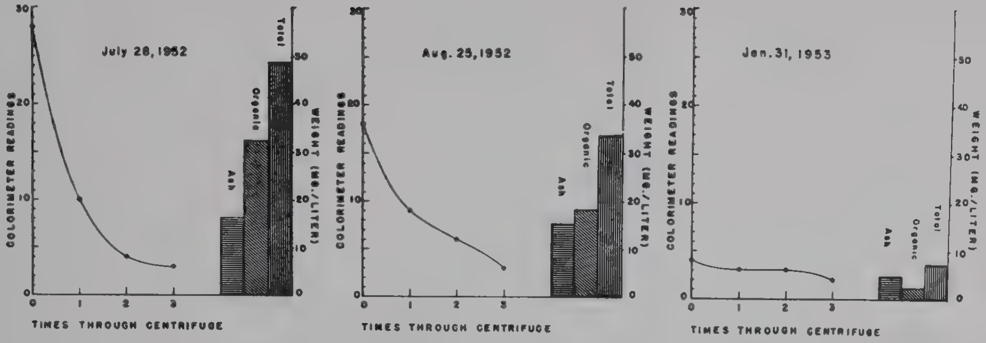

FIG. 1. Results from repeated centrifugation of water from Pymatuning Reservoir. Line graphs show colorimetric readings. Bar graphs indicate weights of residual materials after three consecutive centrifuge runs (average of three determinations).

the colorimeter reading in any of the samples. The phytoplankton community was dominated at this date by blue-green genera, chiefly Microcystis, Aphanocapsa, and Coelosphaerium. At this time of the year species of Cyanophyta comprise about 95 per cent of the phytoplankton, as determined by cell counts.

Centrifugation of water collected under an ice cover on January 31, 1953 showed a reduction in scale reading from four to three after the first centrifugation, and from three to two after the third run. At this time of year the phytoplankton is composed predominately of diatoms and the total quantity of cells is greatly reduced over that found in the summer. Weights indicated in the bar graphs accompanying the scale readings are the results of gravimetric determinations made on the residual material in the centrifuge cup after a liter of water had been passed through the centrifuge three times. The values shown are averages of triplicate determinations which have been corrected for soluble carbonates and dissolved organic substances present in the water retained in the centrifuge cup.

More recently these studies have been continued in a somewhat different manner. Samples of lake water were centrifuged repeatedly, as often as twelve times at the recommended rate, with gravimetric determinations being made on the residue from each run. Typical data from these studies are given in Figure 2 for a summer and a winter sample. In a few instances, particularly when the lake contained large amounts of suspended silt from influent waters, significant amounts of material were removed with the tenth or twelfth run. Generally, however, as in the samples reported here little material was removed after the fifth centrifuging.

Table I presents the results from the samplings of July 11, 1956 and January 30, 1957 as percentages of the fractions removed in each centrifuge run, based on the total amount removed in six centrifugings. From both samples the first run removed about 50 per cent of the suspended organic material and about 80 per cent of the ash fraction. This represents about 65 per cent of the total suspended materials.

Juday (1926) reported that, with the exception of Aphanizomenon, the first centrifuging removes approximately 98 per cent of the organisms usually considered in a plankton catch and that substantially all that remains is taken out by a second centrifuging. He pointed out, however, that silt and suspended organic matter may be continually removed up to the eleventh centrifuging, and possibly beyond. It is further stated that this is apparently colloidal organic matter since all the plankton material is removed from the water by the end of the third centrifuging.

TABLE I. Percentages of materials removed in various centrifuge runs. Calculations based on total amount removed in 6 runs

Centrifuge Run	JANUARY 30, 1956			JULY 11, 1956		
	Total	Organic	Ash	Total	Organic	Ash
1	65.3	50.0	83.6	67.8	50.7	81.1
2	16.2	15.7	17.4	14.8	20.1	10.7
3	8.0	14.3	....	8.6	15.9	2.5
4	7.3	11.4	....	6.4	9.6	4.3
5	3.2	8.6	....	2.4	3.7	1.4
6		. . .	.	....	....	....

While our results are essentially in agreement with these statements for samples taken from the winter community, considerably less efficiency than this is indicated for samples from the summer blue-green community. Reinhard (1931) has reported that algae other than Aphanizomenon may be troublesome in a centrifuge but he concluded that a second passage through the machine was unnecessary. Counts made on samples collected from Pymatuning Reservoir on July 11, 1956 showed that more than 11 per cent of the plankton cells remained after three consecutive centrifuge runs. It should further be noted that the triple-centrifuged water contained not only colonial blue-green genera, but also contained significant numbers of Pedistrum colonies. Results reported in this paper do not necessarily represent the characteristic operation of one individual instrument. Three centrifuges have been used over the past several years and similar results have been obtained with each instrument.

Some modifications in use of the Foerst centrifuge, in interpretation of data collected through standard methods of operation, or in design and construction of the instrument itself, seems necessary. Pennak (1949) used a correction factor of 25 per cent to give greater significance to his centrifuge data from Colorado lakes. Few workers follow his example and some even refer to material collected in one centrifuge run as "total suspensoids." In light of results reported here, a run of three or more times through the centrifuge appears necessary with

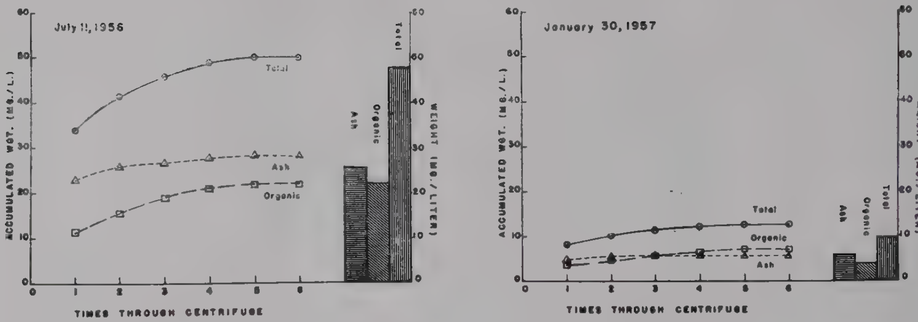

Fig. 2. Line graphs show weights of residual material from Pymatuning Reservoir after repeated centrifugation. Bar graphs indicate weight of residual materials after three consecutive centrifuge runs (average of three determinations).

samples from Pymatuning Reservoir in order to obtain a reasonably accurate estimate of the various fractions of suspended materials.

Suggestions and assistance in this investigation from Thomas H. John and J. Herbert Graffius are gratefully acknowledged.

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FALLOUT ON THE VEGETATION OF NEW ENGLAND DURING THE 1957 ATOM BOMB TEST SERIES[1]

On August 12, 1957, at the completion of a greenhouse experiment involving the use of radioactive phosphorus, control plants expected to be non-radioactive gave counts approximately double the background count. Further study indicated that plants outside the greenhouse were similarly contaminated with assays of grass, tomato leaves, and elm leaves giving counts two to eight times the background count per gram of dry weight.

Contamination with radioactive fallout was suspected and it was decided to continue and expand the investigation while appropriate conditions existed (i.e., while bomb testing continued in Nevada). The objectives of the study were to determine the source of the radioactivity, its local and regional distribution, and the levels of contamination found on plants, and thus describe conditions that should be taken into consideration by investigators using isotopes during bomb-testing periods. It was hoped that the inquiry might also reveal some of the ecological relationships controlling the distribution of fallout.

Except as noted, all counts were made on samples of plant ash. Specimens were oven dried and ashed for three hours at approximately 550°C. Subsamples, usually 100 mg, were placed in steel planchets, leveled with alcohol, oven dried, and then counted in a shielded sample changer containing a 1.2 mg/cm^2 end-window G-M tube coupled to a Tracerlab SC-51 scaler. Most samples were counted long enough to give standard deviations of 5 to 10 per cent; however a few less active samples had standard deviations up to 16 per cent. Counts per minute were converted to disintegrations per minute by calibrating the counter against the constant K^{40} content of KCl, a technique used by the AEC Health and Safety Laboratory for fallout samples (personal communication, I. Whitney). Most of the counts presented are based on an assay of a single subsample. No counts were adjusted for radioactive decay since contamination might have been composed of a composite of fallout materials originating from different blasts.

It seems certain that the primary source of radiation, gross beta activity, was mixed fission products in tropospheric fallout from the 1957 test series in Nevada. This was indicated by absorption curves, a 50 per cent decline in activity in 28 to 48 days, and high $Sr^{89/90}$ ratios, characteristic of fresh fallout, found in samples analyzed by the AEC (Table I). An arbitrary level of naturally occurring radiation in plants, 497 dpm/g ash, was established by radioassaying eight herbarium specimens collected from 1894 to 1956 and presumably free from recent contamination. Plants collected after August 11, 1957, had activities from 1.2 to 39.7 times this arbitrary level of natural radioactivity.

The gross activity of the samples is derived from both internally and externally deposited isotopes. The former

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[1] This work was done as an offshoot of a project supported by NSF Grant 3222.

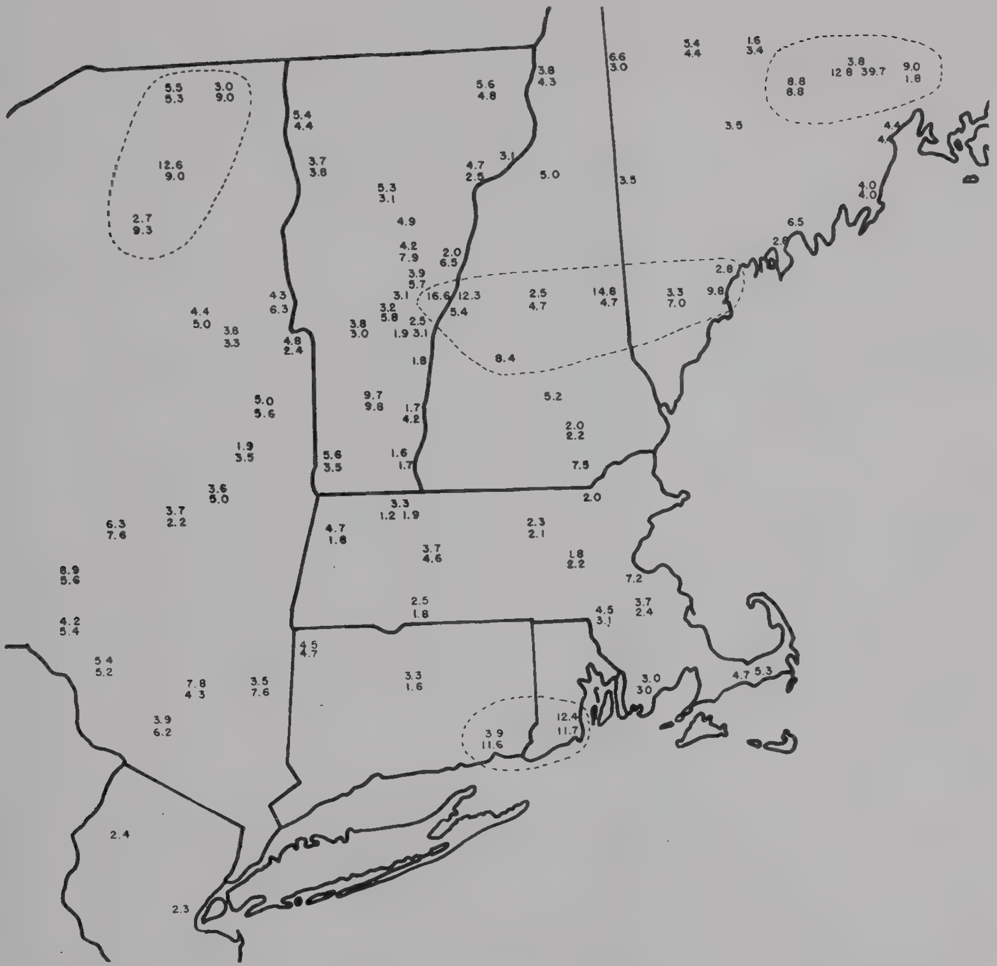
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FIG. 1. Ratios of radioactivity of ashed elm leaves to an arbitrary level of natural radioactivity, 497 dpm/g ash. Pairs of ratios indicate collections made one mile apart. Circled areas indicate regions with a number of higher ratios.

TABLE I. AEC health and safety laboratory analyses

	Total Activity dpm/g Ash	Sr^{90} dpm/g Ash	$Sr^{89/90}$ Ratio	Strontium Units uuc Sr^{90}/g Ca
July 1956 Hay[a]	766	7.75	1.9*	86
June 1957 Hay[a]	771	13.60	0.9*	78
August 1957 Hay[a]	1460	17.30	3.8	97
August 1957 Elm Leaves*	1540	3.42	13.1	13

[a]Average of two samples.
*Single sample.

result from root absorption of naturally occurring isotopes and long lived isotopes accumulated in the soil from previous tests, while the latter result from externally accumulated increments of dry fallout, rainout, and, perhaps, grounded fallout recirculated as dust.

Externally deposited fallout seemed to be the most important source of activity. This hypothesis is supported by an assay of garden and forage plants which showed that the highest activities, 1716 to 3936 dpm/g ash[2], were associated with leaves which have a high surface to weight ratio, while the lowest activities, 623 to 665 dpm/g ash, were found for fruits, which have a much lower surface to weight ratio. The loose superficial nature of part of the contaminants was also demonstrated by the removal of 20 to 53 per cent of the activity from leaves by washing in water for three minutes. The residual contaminants were probably more tightly bound to the surface and/or had been absorbed through the cuticle (Bukovac and Wittwer, 1957). Absorption through the root seems unlikely as a major source of this contamination, since the recent nature of the fallout seems to rule out an extensive cycling through the soil to the roots.

To obtain some information on the extent and level of contamination, 142 samples of American elm leaves, including 61 paired samples picked one mile apart at approximately thirty mile intervals, were collected during late August throughout New England and eastern New York and radioassayed. Inner canopy leaves were collected because they were somewhat protected from scrubbing by the rain and hence presumably have more representative accumulations of fallout. Ratios of sample activity to the arbitrary level of natural radioactivity were calculated and plotted at approximate points of collection (Figure 1). The results showed general contamination in the area ranging from 1.2 (595 dpm/g ash) to the single high value of 39.7 (19,760 dpm/g ash). The average, excluding the latter value, was 4.9 (2435 dpm/g ash). No decay corrections were applied, thus the above figures are underestimates of activity at the time of maximum contamination. Further, it seems quite probable that, due to the limited nature of the survey, contamination higher than that found in the samples occurred but was missed in the sampling process. In addition to the gross regional variations noted in Figure 1, local variations up to a factor of three were observed within 60 per cent of the paired collections. Despite errors inherent in the sampling technique, the data illustrate the difficulty of drawing conclusions about regional and local fallout conditions from data collected at widely spaced stations. In regard to the distribution of fallout in local areas, it would be of interest to know if climatological factors that influence the development of divergent vegetation types (e.g., zones of vegetation on mountains, fog belt vegetation, cove type vegetation, etc.) also influence fallout patterns.

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[2] Dpm's may be converted to counts per minute per 100 mg of ash by dividing by 44.5.

Since the contribution of Sr^{90} to total activity is of considerable interest, samples of hay and elm leaves from the Hanover, New Hampshire, area were submitted to the AEC Health and Safety Laboratory for analysis. Some of the results are summarized in Table I. The hay samples were collected in late August from hay cut, baled, and stored in a barn on dates shown. The AEC states that the values for these samples are not considered excessive and that they are similar to others found elsewhere in the United States (personal communication, I. Whitney).

The August collections had about the same gross activity, approximately double that of samples collected earlier. The difference in activity was probably due to superficial contamination on the August samples. This was suggested by the high $Sr^{89/90}$ ratio for elm leaves and by a recalculated $Sr^{89/90}$ ratio for the August hay.

The strontium 90 content of July 1956 and June 1957 hay roughly paralleled calcium content probably due to more or less indiscriminate uptake of both elements from the soil. Assuming hay collected in August 1957 absorbed a similar amount of Sr^{90} in relation to its calcium content, it seems likely that the increase in strontium 90 over earlier samples was due to superficially deposited recent fallout. Recalculating the strontium $^{89/90}$ ratio for August hay, using a ratio of 1.4 for isotopes absorbed from the soil, a ratio of about 17 is derived for isotopes superficially deposited. This is comparable to the ratio for elm leaves.

The high $Sr^{89/90}$ ratio for elm leaves indicates that the bulk of their Sr^{90} was superficially deposited. If an appreciable fraction had come through the roots, a lower ratio, similar to that observed for August hay, would have been expected. This high ratio may result because there is a relatively little Sr^{90} in the soil under the elm, most of the root system is well below the soil surface where as yet little Sr^{90} is available, or elm has a discrimination mechanism operating against strontium—perhaps retention in the stem nodes as recently suggested by Comar et al. (1957) for other plants.

Although AEC analysis of our samples indicates that, in terms of Sr^{90}, the amounts contaminating plants are relatively small, the possibility of more significant contamination of plants growing in local areas of higher fallout cannot be ignored.

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REVIEWS

Geography of Land and Freshwater Vertebrates[1]

"This book is a geographical, not an ecological, zoogeography. . . . The ecological approach to animal and plant geography is fashionable now, but books written from that point of view . . . are ecologies at heart and hardly geographies at all. I do not mean to make little of ecology, but just to say that it is not zoogeography . . . I have described and discussed the distribution of land and fresh-water veterbrates as fully as I can, and I have cut many other subjects to bare references or just statements of my point of view." Thus Darlington defines the scope of his book, which is—wisely—more limited than its title. Within that scope, this important, up-to-date treatment is a fully worthy successor to the classic works of the Sclaters, Wallace, and Matthew. It is greatly superior to the only other recent book in just the same field (de Beaufort, 1951).

Over half of the book is devoted to descriptive zoogeography and factual data, with separate chapters on the freshwater fishes and on each of the four primarily terrestrial classes of vertebrates. A detailed appendix to each of these chapters gives the distributional facts in systematic order for all living and some extinct families, plus well-chosen lists of references. The last five chapters then discuss broader conclusions and more theoretical matters: continental patterns; island patterns; the evolution of those patterns; their relationship to geological history; general principles and the geographical history of man.

Darlington's major points, although not given in just this way or sequence by him, may be summarized as follows:

(1). The existing distribution of vertebrates has evolved under geographical circumstances essentially like those of the present time. The continents have been stable in identity and position. Variable major intercontinental bridges (hence dispersal routes) have existed between Asia and North America, North and South America, but nowhere across the Atlantic or directly between any two southern land masses.

(2). In accordance with this geographical pattern, east-west and west-east dispersals have occurred mainly across North Africa-Eurasia-(Bering Bridge)-northern North America. North-south dispersals have occurred separately down continental axes to South Africa, Australia (to Tasmania), and South America.

(3). Most islands other than those recently parts of continents (such as: Sumatra, Trinidad, British Isles, Japan) have received their nonmarine faunas by overseas dispersals. Island faunas resulting from such dispersals are impoverished and more or less random in taxonomic and temporal origins. The West Indies (except Trinidad), Madagascar, and the Galápagos, for example, have such noncontinental faunas. (Darlington gives adequate reasons for not following the classical usage of calling these faunas "oceanic.")

(4). Dominant groups of animals tend to originate in major land areas and to radiate outward from there. There is faunal attenuation northward, southward, and outward (e.g. to islands) from such centers. Shrinking or ultimate extinction of local nondominant or earlier dominant groups accompanies the expansion of new dominant groups. Local differentiations, re-radiations on successively smaller scales, and other factors make the details incredibly complex without, however, obliterating the main underlying pattern. Success in competition defines dominance, and competition is a or even *the* basic over-all dynamic of evolutionary zoogeography.

(5). Most of the important, successively dominant, groups of vertebrates have originated in and radiated from the Old World tropics.

Darlington's points (1), (2), and (3)—as here listed—are in essential agreement with the then highly controversial views published in 1915 by the late W. D. Matthew. Point (4) involves some difference of viewpoint but no fundamental contradiction. Matthew's evidence and treatment were much less complete than Darlington's and involved some errors, but he was clearly and earlier correct as to those principles. It is most welcome to have these of Matthew's views placed in a virtually unassailable position by Darlington's work. It is natural and even useful that Darlington's agreement with Matthew is largely implicit and that he more explicitly stresses points on which he does not agree. Matthew maintained that successive radiations would tend to push earlier, hence more primitive, groups into peripheral areas, which means mainly into the far south (and to some extent onto islands) because the dead ends are there. Darlington is not quite conclusive or even completely clear on this point, but his tendency is to reject Matthew's generalization.

Darlington's point (5), as listed above, is given in strong dissent from Matthew's view that most (of course not all) dominant groups arose in and radiated from the Northern Hemisphere, especially in the North African-Eurasian-North American temperate zone, and that movement outward (mainly southward) from that zone was influenced by changes in climate through the Cenozoic. Darlington admits but perhaps undervalues the fact that such climatic changes certainly did occur. The always vague tropical-temperate transition was neither so sharp nor so far south in the early Cenozoic as it is today. Hence the disagreement as to tropical or temperate origins may not be as clear-cut or meaningful as it sounds. The disagreement as to mainly Old World origins or Old and New World, together, is also not really very important. Matthew also stressed Old World more than New World origins, without excluding the latter. And here Darlington's evaluations are sometimes dubious. For instance, he says that "the ancestor of the family [Antilocapridae] presumably came from Eurasia," but there can hardly be any question that the family, as such, arose in North America. Matthew based this part of his theory mainly on homeotherms and probably overgeneralized in extending it to poikilotherms. Darlington perhaps similarly overgeneralizes from poikilotherms to homeotherms. A reconciliation of the two theories, in as far as they really do differ, seems possible and desirable.

Discussion of the relationships between Matthew's and

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[1] Darlington, Philip J., Jr. 1957. Zoogeography: the geographical distribution of animals. New York: John Wiley & Sons, Inc.; London: Chapman & Hall, Ltd. xi + 675 pp., 80 figs. $15.00.

Darlington's views is an act of justice, but it must be emphasized that Darlington's book is not only more than forty years more modern but also incomparably more detailed and, in its details, somewhat sounder. It essentially supersedes all earlier reviews of its subject, and is henceforth indispensable for all biologists, specifically including ecologists. While wisely eschewing consideration of small-scale zoogeographical phenomena that are primarily ecological, Darlington makes clear the over-all involvement of ecology in his large-scale zoogeography. The book is, moreover, a pleasure to read and to use. It is beautifully written, at a technical level but without obscurantism and even with some appropriate humor, and it is soundly organized for reference. It is not only by all odds the best available work on its subject but also one of the outstanding books on any science in recent years.

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Zoögeography of Land and Water

The British series of Textbooks of Animal Biology has issued two complementary books which cover the realm of animal distribution throughout the entire world. L. F. de Beaufort[1] has written on the zoögeography of land masses and bodies of fresh water, while Sven Ekman[2] has prepared a text on the zoögeography of all oceans and seas. The two books have much in common. Both are world-wide in coverage, are descriptive and comparative in nature, are developed from a regional point of view, and stress the importance of historical zoögeography. Neither one is much concerned with the dynamics of animal distribution, although plausible ecological interpretations are occasionally suggested to explain a particular pattern of present distribution. Land bridges are frequently postulated as a possible solution to some problems of distribution, especially in the de Beaufort text. Animal evolution and ecological subspeciation are also considered, but the main emphasis has been placed on the determination of endemic organisms and the factors of physical and historical geology which attempt to explain such endemism. The books are necessarily compilations from the world literature on regional faunas and animal distribution. A wealth of information is presented to the reader, and many problems for further study and investigation are evident in both books. A knowledge of certain family and generic names is essential for understanding much of the discussion. Vernacular names in English help to place many of the taxonomic names used, but often this is done in only a very general way. Theories of distribution are occasionally quoted, and where there has been lack of agreement in published literature, a synopsis of the controversial points is given without critical treatment or an attempt to settle the issue.

Zoögeography of the Land and Inland Waters contains chapters on the Holarctic, Oriental, Ethiopian, Neogaea (South American) and Notogaea (Australian) regions with other chapters on certain island groups—the British Isles; Madagascar and neighboring islands; and Celebes, the Moluccas, and the Lesser Sunda Islands. The author was Professor of Zoögeography at Amsterdam, as well as former Director of the Zoological Museum, and has followed more or less the classical system of P. L. Sclater.

Attention is given primarily to the vertebrate groups, although occasional mention is made of some invertebrates which illustrate endemism or a particular type of distribution. Paleontology, as well as historical geology and geography, is drawn upon for support of explanations of distribution. The author is guided by his statement in the introduction to his work that, "the existing distribution of animals depends not only on the present but on the past." Glaciation and former land bridges play conspicuous roles in this book of historic zöogeography. Most of the ten illustrations are maps of distribution, a larger number of which would have been desirable. There are 132 references, primarily to publications in English, French, and German, and a complete index.

Ekman's book on Zoögeography of the Sea is a much larger work and contains many more illustrations. It is a translation from the Swedish by Dr. Elizabeth Palmer. Professor Ekman was formerly Professor of Zoölogy at the University of Uppsala and a specialist in marine zoögeography. He describes the warm-water fauna of the shelf; the Mediterranean-Atlantic fauna, the Sarmatic fauna, boreal fauna of the North Atlantic, temperate fauna of the North Pacific; the Arctic fauna; the warm-temperate faunas of the southern hemisphere, and the antiboreal faunas. He then discusses longitudinal distribution and bipolarity, deep sea faunas, and pelagic faunas. Many outline maps are presented, but the book would be greatly improved with end papers showing the water masses and ocean currents of each hemisphere which are mentioned in the text. The systematic groups which receive major emphasis are the sponges, coelenterates, polychaetes, crustaceans (especially the decapod crustaceans), mollusks, echinoderms, ascidians, and fishes. Aspects of paleozoology as well as recent faunas are often considered, the former as a prelude to the latter. Nearly 600 references are given to literature citations in many languages. There is a complete index.

These books summarize a good deal of present knowledge, and form a good foundation for future work on zoögeography and the dynamic causes of animal distribution. They portray the past, bring some major distribution patterns up to date, and set the stage for ecological research. Professor Ekman wrote in his last sentence, "biogeography cannot confine itself simply to describing the occurrence of living forms, arranging them regionally, investigating the ecological causes of distribution. It must also proceed historically." The two books reviewed here do much to fulfil this need and exemplify well that point of view.

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[1] de Beaufort, L. F. 1951. Zoögeography of the land and inland waters. London: Sidgwick and Jackson, Ltd. viii + 208 pp., 10 figs. $5.00. (U. S. agent—Macmillan Co., N. Y.)

[2] Ekman, Sven. 1953. Zoogeography of the sea. London: Sidgwick and Jackson, Ltd. xiv + 417 pp., 121 figs., 49 tables. $6.50. (U. S. Agent—Macmillan Co., N. Y.)

GEOLOGICAL ECOLOGY[1]

This book has three parts: the first consists of six introductory essays on paleoecology, the second contains seventeen paleoecological analyses from the fossil record and the third is an annotated bibliography of marine paleoecology.

To an ecologist's eye the first part of the book is the most attractive. Among a number of valuable expositions of the history and methods of paleoecology, the classification of marine environments and the organic constituents of fossils, E. S. Barghoorn's piquant discussion of the origin of life stands out as a particularly engaging treatment of a subject that has attracted many gifted writers.

The analyses in the second part display much ecological sophistication on the part of some of the authors but considerably less on the part of most. Marine paleoecology is a very difficult subject and the geologic data usually do not permit firm inference about the nature of the past environment. It is rarely possible to advance beyond such inferences to consider the relationships of organisms and environment that constitute the subject of ecology. Too many of the contributors, apparently unaware that such an advance is possible, regard ecology as the cataloguing of environmental properties and paleoecology as informed guessing about the properties of past environments. Too few have displayed the critical sense of the authors of the chapter on paleoecology of the Precambrian of Northwestern North America, who begin with the statement: "Precambrian formations of Northwestern North America contain no fossil assemblages suitable for ecological analysis."

The bibliography is divided on a taxonomic basis with some geographic and temporal subdivisions. Each section is prefaced by an introduction and each bibliographic entry is provided with a brief summary. Little of this material is ecological and some is not even concerned with the sea. Although there are a few meritorious exceptions most of the sections suffer from the usual fault of American bibliography: almost all the articles cited are in English.

The growing awareness of ecology among geologists holds great promise for both ecology and geology. Unfortunately enthusiasm for the new discipline sometimes tends to outrun understanding of it, so that the label of paleoecology is applied to material that is and always has been the essential substance of historical geology. It is disappointing to see this unhappy side of the trend to ecology reflected in the present work, especially as its editor is a distinguished marine paleoecologist.

Despite its shortcomings the book summarizes much useful material. Its publication has been subsidized by the Penrose Fund, and the buyer gets a huge volume for his money. It contains a large amount, though a small proportion, of ecological information, and documents in embarassing detail our ignorance of marine paleoecology. Ecologists interested in the sea's past should find it a worthwhile investment.

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DUKE UNIVERSITY

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[1] Ladd, Harry S., editor. 1957. Treatise on marine ecology and paleoecology. Volume 2, Paleoecology. (Symposium) New York: Geological Society of America, Memoir 67. x + 1077 pp., num. figs. $10.00.

A DIGESTIBLE ANIMAL ECOLOGY FOR ADULTS[1]

In June, 1957, the Cold Spring Harbor Symposium on Quantitative Biology dealt with a predominantly ecological topic for the first time in its history. Macfadyen's book constitutes a statement of why this recognition of the field is deserved. Avowedly neither an elementary text nor an encyclopaedic treatment of the subject, the book is designed to replace Elton's classic.

Macfadyen's thesis is that the population is the proper unit of study for animal ecologists, and his development of this thesis is impressive. The subject is treated in three parts: The Ecology of Individuals (62 pp.), Animal Population Ecology (78 pp.), and Properties of Animal Communities (104 pp.). In the first part, the author indicates the kinds of information to be obtained from autecological studies. Since these are primarily concerned with preferences and tolerances of animals, the longest chapter treats microclimates and ways to measure them. Macfadyen concludes that the autecological approach suffers from three defects: first, the fact that only the extremes of a niche can be indicated by a set of physical factors; second, the lack of ". . . methods for analysis of the interrelations *between* species of animals, and this kind of relationship is hardly touched by autecological techniques"; and third, the inability of the method to indicate factors controlling the population size and hence the importance of a species.

Part II opens with chapters on methods of collection and the estimation of animal numbers. These chapters include excellent treatments of the degrees of accuracy obtainable and the sources of error in several well-known methods. There follows a consideration of demography, in which the parameters of populations are described, and indications given of the methods used to estimate them. The reader is next led carefully through the food-chain—biomass—productivity—efficiency concepts, with emphasis on the meanings that have been given to the various terms by different authors. The chapter ends with an argument favoring metabolic activity over biomass as a measure of production. Aside from an equation that is almost certain to confuse the "naturalist, the student, and the layman" to whom the book is addressed, the chapter on the metabolism of populations is thoroughly stimulating. Of particular interest is the comparison in a hypothetical meadow of the relative importance of different animal groups, as based first on numbers of individuals, then on biomass, and finally on metabolism.

At the beginning of Part III, four chapters on population dynamics treat mathematical, experimental, and field investigations both at the intra- and interspecific levels. Pointing out the advantages and limitations of each approach, Macfadyen covers the field patiently, and by referring to the same work in different contexts manages a nice coherence. The reader becomes aware of numerous controversies, from density dependence to population cycles, without being made to feel that he must take sides.

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[1] Macfadyen, A. 1957. Animal ecology: Aims and methods. London: Sir Isaac Pitman & Sons, Ltd. xx + 264 pp., 18 figs., 6 plates, 11 tables. 40/-, $5.65.

or that the controversies are likely to be settled shortly.

The chapter on "biocoenology" is less satisfying than the rest of the book, but this is probably a reflection of the field rather than of the author. In it, he describes various methods that have been employed in the detection and delimitation of communities, and discusses the question of the co-extension of plant and animal communities. He concludes that too much work has followed plant community methods and concepts uncritically, and argues that although much can be done in delimiting animal communities, more understanding will come from detailed information about the biological links between the organisms inhabiting the same localities. A brief chapter on the community is concerned primarily with definitions. Macfadyen tries to avoid both the noncommittal (and therefore useless) and the "organismic" definitions, although he leans toward the latter. He concludes that we do not have enough information to define it properly, but regards the term community as a label for a working hypothesis that "includes the properties of species constancy, dynamic stability, and organismic unity." There is a plea, accompanied by typical "horror stories," for ecological understanding before control of natural populations is attempted, and the book closes with a summary of the author's ideas about promising methods and the most fertile fields of investigation.

Macfadyen's personal interest in soil zoology is reflected in the numerous examples taken from this area, and their presence makes for freshness. Throughout the book, he has labeled his own opinions clearly, and has not hesitated to express them, although he has presented both sides of a number of controversial issues. The thesis approach gives the work a coherence that is unique among current ecology books, but as the author freely confesses, it also makes for one-sidedness, so that some readers will look in vain for a treatment of their pet subjects.

The book's faults are minor compared with its virtues, and are mostly concerned with the rather numerous editorial and/or typographical errors. This criticism applies even to the lengthy bibliography, which otherwise would be exceptionally valuable, as it includes many references to work done on the continent of Europe, which the American ecologist often misses.

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RECENT ADVANCES IN INVERTEBRATE PHYSIOLOGY: A SYMPOSIUM[1]

This book includes the edited presentations of sixteen participants in a symposium held at the University of Oregon campus in September, 1955. Although not attempting to cover completely the broad field of invertebrate physiology, major emphasis of the symposium appears to have been centered especially upon endocrine mechanisms and neuromotor function in invertebrates, particularly arthropods. Notable by its absence from the panel of subjects covered is the highly active research area of invertebrate metabolism, especially the metabolism and biochemistry of flight and the giant mitochondria of insect flight muscle. Among the excellent papers, particularly stimulating are the reports on Neuronal Integrative Mechanisms by an outstanding worker in this field, T. H. Bullock, on Neurohormones by John Welsh, on Invertebrate Renal Function by A. W. Martin, and on the Rhythmic Nature of Life by F. A. Brown, Jr., who has firmly established the concept of biological clocks in contemporary biological thinking, through his extensive and provocative studies on the rhythmic behavior of a variety of animals and plants. The ecologist will be especially interested in the presentations of Passano on Predator-Prey Recognition in Lower Invertebrates, by Mittelstaedt on Prey Capture in Mantids and by Baylor and Smith on Diurnal Migrations of Plankton Crustaceans, as well as the earlier-mentioned paper by Brown.

Well-written and well-edited, this book is an excellent reference volume on a rather restricted number of areas of interest in which active research is currently under way, in invertebrate physiology, ecology and biophysics. Most of the reports represent summaries of the individual research findings of each author; several, however, are reviews of the writer's own work as well as of the early and recent work of others in such research. This makes for a certain degree of versatility in the subject matter's treatment as well as heightened interest in several cases. It also enhances the value of this edited volume as a reference book. General invertebrate zoologists, physiologists, and ecologists will find this book a lucid and interesting compilation of the background for and latest ideas in several of the more active areas of research in invertebrate zoology.

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[1] Scheer, Bradley T., editor. 1957. Recent advances in invertebrate physiology. A symposium. Eugene: University of Oregon Publications. vi + 304 pp., 9 figs. $5.50.

AN ELEMENTARY TEXT OF BASIC ECOLOGY[1]

Dr. Ralph Buchsbaum and his wife have prepared an elementary text in ecology for use on the college freshman level. This new work is an intermediate step in their production schedule. On the one hand it is an expansion and improvement of a booklet entitled READINGS IN ECOLOGY published by the senior author twenty years earlier, while on the other hand it is a testing ground for a forthcoming book of larger proportions.

The present work is clearly and simply written, and it is illustrated with the numerous excellent photographs and diagrams which always characterize the publications of the Buchsbaums. Most of the photographs were taken by the authors in many and ecologically different parts of the world. Unfortunately a few photographs are not clearly reproduced, a situation usually associated with the photographic off-set method of printing employed in this book. This method also leaves the right-hand margin of the text in uneven form, although this feature is not objectionable. The illustrations are not numbered and are seldom referred to in the text, but they are so carefully placed that they become an integral part of the text. Examination of the photographs and reading of the legends becomes an automatic and logical process in reading the book.

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[1] Buchsbaum, Ralph, and Mildred Buchsbaum. 1957. Basic ecology. Pittsburgh, Pa.: The Boxwood Press. ix + 192 pp., 183 figs. $2.35 with paper and $3.50 with cloth cover.

The scope of this little volume is very wide, including plant, animal, and human ecology. As the title indicates, it is concerned with basic principles. It is largely descriptive in nature and concerned more with an over-all view of field observational relationships than with experimental or laboratory studies. Attention is often directed to possible practical applications of ecological knowledge to problems of mankind. There is a brief bibliography of general works in the major branches of ecology and a good index. The authors have chosen to use the English rather than the Latin form for the plural of such words as larva (i.e. larvas).

The only question this reviewer would raise is the desirability of placing all marine communities into a single biome. Considering the vast differences among marine communities and the tremendous range in environmental conditions from shoreline to ocean deeps throughout the world, such a grouping does not seem reasonable. The reviewer would agree to classify all deep ocean-bottom communities together, but not all marine communities.

For an introduction to the nature, and to the general principles, methods, and applications of ecology, this little book is admirable. Fortunately its price is within the range young students can afford. Undoubtedly this little book will do great service in stimulating interest in ecology among college students and laymen.

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THE FOREST AND THE TREES[1]

The broad meaning of the facts of a given study should assume importance to a student beyond the facts themselves. But often such values escape appropriate emphasis. This is true in biology, young students of which seem prone to miss, for instance, the implications of biological thought and fact on human affairs. The need has been great for a textbook of biology that emphasizes both the forest and the trees and makes each more understandable in the light of the other. Such textual support is valuable to the best of teachers. There is now available such a book, organized around evolutionary, which is to say ecological, thought. Moreover, it is masterfully, intelligently, and gracefully written. No reader of LIFE could possibly escape relating himself, and the groups of which he is part, to his local environment, and, indeed, to the life of the world.

Nearly one-third of this superb book is devoted to ecological material, partly because it is biology and partly to give the background for elaboration of the unifying theme of biology, organic evolution. But more importantly, the ecological point of view is present on almost every page; the authors make clearly evident that this approach is in fact a way of life, and not merely a subsection of a textbook (and thus of a "course"), which has to be examined simply because it is there. This book stands alone; it is almost the only logical choice for use with students of introductory biology or zoology.

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[1] Simpson, George Gaylord, Colin S. Pittendrigh, and Lewis H. Tiffany. 1957. Life: an introduction to biology. New York: Harcourt, Brace and Co. xiv + 845 pp., num. figs. $6.75.

A CONSERVATION PRIMER[1]

Most professional conservation workers will probably acknowledge that their field is approaching a rather critical point. The outcome of such matters as the controversies over the Echo Park and Panther Dams suggests a strengthening of public desire for over-all balance in resource use, but it is alarming to many of us to see the extent to which emotion rather than calm reckoning of facts decides the issues. The Natural Resources Council of America has undertaken what must necessarily be a long uphill struggle to put this awakening public conservation conscience on a firm factual base and is to be commended for its little volume, AMERICA'S NATURAL RESOURCES, which is meant to serve as an important step in the campaign.

The book sets out to provide fundamental information for the citizen-conservator on each of the major natural (i.e. renewable) resources and to assess the progress that has been made in the United States toward solving the many serious problems involved. Following introductory chapters on the ecological approach to conservation by Shirley Allen and on the relation of human populations to renewable resources by Fairfield Osborn, separate chapters are devoted to each resource field. It is pleasing to see that the field of "Parks and Wilderness" is granted full membership in the list rather than being given a generous half-paragraph in the "Forests" section, as is often the case. The book ends with an admirable restatement of land use principles by E. H. Graham and a convincing plea by Ira N. Gabrielson for a broadly inclusive natural resources policy.

In view of the indisputable excellence both of the panel of authors and of the aims of the book, it is puzzling that the job does not come off more effectively than it does. Space is limited, to be sure, and there are occasional lapses into undisguised preaching, but these are not necessarily weaknesses. The major difficulty seems to be that the authors try only rarely to escape from the overly generalized style that is the curse of conservation

[1] Callison, Charles H., editor for the Natural Resources Council of America. 1957. America's natural resources. (Symposium) New York: The Ronald Press Co. v + 211 pp. $3.75.

writing. Surely, the number of American citizens that needs to be told that wildlife needs cover or that floods and erosion are almost universal problems is small!

For the highly motivated devotee of conservation this book will serve a useful function, particularly in expressing the unified, ecological point of view that is overtaking all aspects of resource management. Others, regrettably, may be left, bored, by the wayside. For the professional conservationist there is food for thought, not so much in regard to the subject matter itself but to the way in which is is presented. Two chapters in this rather discouraging collection of generalities are worthy of particular note. The one on grasslands by David Costello probably has more immediately useful information than any other; but the best job of relating principles to cases to recommendations comes in the field which has always seemed to this reviewer to be most severely addicted to the thundering platitude. In their chapter on "Fish," Albert S. Hazzard and William Voigt, Jr., have not only provided the necessary generalized picture but have amply fortified it with interesting and meaningful detail. Other conservation writers might well take heed.

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CALIFORNIA RANGE LAND[1]

The author has written an original and distinctive book on grassland ecology. He has combined both the history and ecology of California range lands into a very meaningful and interesting discussion. His historical references date from the early sixteenth century until the present. The effect of four centuries of settlement is very clearly portrayed by this complete and vivid account. Man and his animals, along with limited and irregularly distributed precipitation, have drastically changed the vegetation of California grazing lands. Native species of grasses were quickly replaced by plants introduced by European settlers, until today the once beautiful perennial grass range described by early Spanish explorers is almost entirely covered with introduced annual grasses. Effects of early settlements on grasslands have often not been thoroughly studied or understood. Similar studies in other areas on the history of past use would undoubtedly reveal some influences of early mismanagement.

The author gives a very complete picture of California's range resource. He first describes the physiographic regions of the state relating the variations in precipitation, temperature, soils, and other factors. The reader is then given a very complete picture of the distribution of the many plant associations in California as well as a good discussion of the environmental factors that regulate their size and distribution. He lists the coniferous forest, oak woodland, coniferous woodland, California prairie, chaparral, sagebrush, desert scrub, and marsh grass as the principal plant associations. Excellent maps and photographs are used to illustrate these communities as they existed in pristine and recent times. A realistic account of the present-day range resource is included in the discussion of these associations.

Since new plants dominate the landscape new methods of using these grasslands have had to be developed. Ranchers had to learn how to use annual grass ranges so that they could depend on a sustained production of forage. Various methods of range improvement that are being used to "reverse the trend" of degeneration are described in one of the last chapters in this book. They include control of undesirable woody vegetation, range revegetation, range fertilization, grazing management, forage utilization, and inventory of wild land resources.

This book is made more valuable by the excellent illustrations and tables throughout the text. There are sixteen plates which, for the most part, illustrate the plant associations described by the author. Some plates serve to illustrate changes that have taken place since the state was settled. Thirteen of the eighteen figures in the book are maps, both vegetational and graphic. Two enlarged maps of pristine and present-day associations are placed in a folder attached inside the back cover of the book. Other figures are primarily graphs. Thirty-four useful tables are distributed throughout the text, and other statistical information can be found in the appendices. The printing is excellent.

This study, in its placing of present ecology in historical perspective, is related especially to Malin's[2] work on grassland history. Like Malin's work, it shows that the historical approach may add a great deal to the value and interest of the ecological evaluation of range lands, and that such historical interpretation is an important avenue of ecological research.

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[1] Burcham, L. T. 1957. California range land. An historico-ecological study of the range resource of California. Sacramento: Division of Forestry, Department of Natural Resources, State of California. 261 pp., 16 plates, 18 figs. $3.12.

[2] Malin, James C. 1956. The grassland of North America: Prolegomena to its history. 3rd printing. Lawrence, Kans.: J. C. Malin. 469 pp.

AICHINGER'S SYSTEM: VEGETATION DEVELOPMENT TYPES[1]

In a series of monographs initiated in 1951, Erwin Aichinger and his co-workers present a new system of practical phytosociology as it applies to the vegetation of Carinthia, in Austria.

Aichinger is a forester who wants to gain practical information from the investigation of plant communities. A strict follower of Braun-Blanquet at the outset, as shown by his 1933 publication on the vegetation of the Karawanken, he eventually came to realize that, in his region, the Zürich-Montpellier system was of little value to practicing foresters. These were shown, during phytosociological short courses, carefully selected examples of the various associations and subassociations with their full complement of character-species. Unfortunately, once they returned to their own forest districts, they found little or no relation between the teachings and the actual field situations. In the first place, character-species are often eliminated as a result of clear-cutting, thinning, planting, introduction of exotic species, litter removal, grazing, etc. Then, in mountain country, the significance of a given character-species may vary, depending on the altitudinal zone in which it is found. Moreover, many character-species do not reflect the environmental conditions but are the expression and the result of competition or floristic history.

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[1] ANGEWANDTE PFLANZENSOZIOLOGIE [WIEN]. 1951-. Publications of the "Institut für angewandte Pflanzensoziologie des Landes Kärnten," edited by Erwin Aichinger and published by Springer-Verlag, Vienna. Volumes I-XVI published to date. Each volume priced according to size, at about 4 cents per page. Not to be confused with the series of the same name edited by R. Tüxen, published in Stolzenau/Weser, Germany, reviewed by A. W. Küchler in ECOLOGY 38: 541-542, 1957.

Because foresters cannot restrict their activity to those few model stands where character-species abound, Aichinger proceeded to devise a system which would apply to any forest, no matter how disturbed, and even to plantation stands.

The system is explained in three articles of Volume I of the series (1951), two of them by Aichinger himself ("Vegetationsentwicklungstypen als Grundlage unserer land- und forstwirtschaftlichen Arbeit," pages 17-20, and "Soziationen, Assoziationen und Waldentwicklungstypen," pages 21-68) and one by G. Wendelberger ("Das vegetationskundliche System Erwin Aichingers und seine Stellung in pflanzensoziologischen Lehrgebäude Braun-Blanquet's," pages 69-92). In addition, the volume ends with a 16-page glossary (pages 171-186) that includes Aichinger's special terminology as well as general phytosociological concepts.

The method used for sampling and describing plant communities is that of Braun-Blanquet. One square plot, 10 meters on the side in forest vegetation, is taken in a "typical" area of the stand. Records are made of location, elevation, exposure, degree of slope, major soil characteristics, cover, and stratification. The species found are listed and assigned coefficients of abundance-dominance and sociability.

The similarity ends there, however. Sampling data are not compiled in association tables for the detection of character-species and subsequent classification in classes, orders, alliances, associations and subassociations.

The highest unit, for Aichinger, is based exclusively on the physiognomic-floristic characteristics of the upper stratum. For example, all spruce forests (to the exclusion of plantation stands which are classified on the basis of their natural vegetation) are included in the super-group ("Obergruppe") *Piceetum excelsae,* all mixed fir-beech stands belong to the *Abieteto-Fagetum.*

The next breakdown is purely ecologic. On the basis of differential species which indicate some prevailing feature of the habitat, super-groups are subdivided into groups ("Gruppe"). These are distinguished by epithets that reflect soil acidity (*acidiferens, basiferens*), parent material (*calcicolum, silicicolum*), water relations (*paludosum, inundatum,* etc.), or even certain manifestations of human influence, (*regerminatum* for a coppice forest, *secondarium* for a second-growth forest).

The basic unit of the system, the vegetation development type ("Vegetationsentwicklungstyp"), is determined strictly by dynamic criteria. Information derived from 1) the presence of ecologic-syngenetic differential species, such as relics of a preceding stage or pioneers of a new stage, 2) evidence of past disturbances (grazing, litter removal, erosion, etc.) is combined with knowledge of the general environmental conditions of the group to assign the stand to a successional series.

The development types may be further subdivided into subtypes on floristic-sociologic grounds. The presence of a species in the upper layer, in sizable but minor proportion, is indicated by the suffix *-etosum* (*e.g., Piceetum-Pinetosum silvestris*), whereas species, or groups of species, dominant in the lower synusiae are denoted by the suffix *-osum* (*e.g. Pinetum silvestris ericosum carneae,* or *Fagetum silvaticae herbosum, i.e.* rich in herbs).

In many cases, the developmental series includes at least three terms: the stage under study, the one that immediately preceded, and the one that is most likely to succeed. For example, the sequence *Ericetum carneae* ↗ *PINETUM silvestris ericosum carneae* ↗ *Piceetum excelsae* refers to a Scotch pine stand with an undergrowth of *Erica carnea,* derived from an *Erica* heath and evolving toward a spruce forest.

If the community under study is considered as self-perpetuating, barring human interference, it will of course be listed at the end of the series, whether it is a "Schlussgesellschaft" (climatic climax) or a "Dauergesellschaft" (edaphic or physiographic climax).

Progressive successions are indicated by arrows pointing upward; regressive successions, mostly due to anthropic site deterioration, are expressed by arrows pointing downward. One short bar on the arrow denotes the initiation of successional change by clear-cutting, whereas three bars indicate that the stand was subjected to a coppice silvicultural system.

The existence of primary and secondary, autogenic and allogenic successions (in Tansley's sense) is implicity recognized, but more emphasis is placed on the determination of the terms of the successional series. Several stands, identical in composition, may conceivably belong to as many developmental series and thus be considered as different vegetation development types. Each stand is treated on its own merits and there is no attempt to establish abstract concepts of given development types.

Aichinger developed his unique system with a practical purpose in mind in a region with a forest climax, a strong relief, and where human influence has been overwhelming. Avalanches, landslides, and wild streams are constantly changing the land surface. Wide differences in elevation, exposure, degree of slope, and parent material greatly modify the environment over small areas. Man has cleared forests, disturbed the remaining ones by removing litter, mowing, grazing cattle, cutting selectively, and by introducing species outside their natural altitudinal zone. Hence the preoccupation with vegetation dynamics, the importance given to physiography, the lack of concern for theoretical considerations, the pragmatic approach, and the flexibility of the system.

So far, the following plant communities have been analyzed by Aichinger: beech forests (Volume V, 106 pages, 1952), Scotch pine forests (Volume VI, 68 pages, 1952), spruce forests (Volume VII, 179 pages, 1952), *Calluna* and *Erica* heaths (Volume XII, 128 pages, 1956), shrub types (Volumes XIII, 84 pages, and XIV, 171 pages, 1957). Each publication usually starts with general considerations on the ecology of the super-group and its breakdown into groups (*e.g. Fagetum basiferens, acidiferens,* etc.). This is followed by representative case histories with stand description, phytosociological data, assignment to successional series, and silvicultural recommendations. Some of the illustrations are very good, others could have been omitted. The text is often wordy and repetitious, and there are inconsistencies in the nomenclature of vegetation development types.

Despite these minor shortcomings, these publications, particularly the theoretical papers of the first volume, should be studied by all those interested in vegetation science. In this reviewer's opinion, Aichinger has made a significant, original contribution to synecology. Although he still claims allegiance to the Zürich-Montpellier school, he has actually abandoned its basic concepts (fidelity, character-species, vegetation units) to retain only its analytical procedure and part of its vocabulary. His empirical approach might be compared to that of Egler in this country. With Tüxen, Ellenberg, de Vries, and many others, but using different methods, he represents the applied phase of phytosociology which is now quite important in Europe.

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VEGETATION OF SOUTHWEST GREENLAND[1]

The main task of the expedition of T. W. Böcher to Southwest Greenland in 1946 was the analysis of plant communities as a basis for treatment of the composition and ecology of the vegetation and discussion of principles.

Böcher states that he cannot subscribe to the views of Braun-Blanquet in classifying vegetation, particularly the use of character-species. Nordhagen, in Norway, he indicates has made improvements, giving a basis to build further. Böcher classifies species into four groups as a basis for the characterization and demarcation of vegetational units. ". . . the choice of a species to be used for classification must be preceded by a much more thorough study than the majority of research workers have hitherto made" (p. 8). The first of these groups, "Area-geographical differential species," consists of species which by their presence or absence in similar climatic and edaphic conditions in various geographic areas differentiate "related" communities. For example, species associated with *Alchemilla pentaphyllea* differentiate snow-patch vegetation in the Alps from similar communities in Scandinavia.

The second group, "Climatic indicators," comprise species which because of their occurrence in a certain macroclimate give the community "a definite ecological-climatic affinity." For example, *Sarothamnus scoparius,* a species with suboceanic southern distribution aids in segregating Danish *Calluna* heaths in which it occurs from those without southern species, such as *Calluna-Vaccinium vitis-idaea* heaths. In the group "Ecological differential species" are species which occur in habitats possessing a definite combination of micro-climatic and edaphic factors. *Potentilla tridentata,* in continental parts of Southwest Greenland, contributes to differentiating the rock community from other xeric communities without rock plants. The group, "Ecogeographical guiding species," consists of species that belong to a "definite biological type as well as a definite biological distributional type." *Pulsatilla pratensis,* for example, a southern continental xerophyte, is useful in classifying Danish communities to show resemblances to steppe vegetation, while *Jasione montana* indicates suboceanic dry grassland.

In characterizing communities Böcher lists species that belong to each of these groups. For example, in the *Juncus trifidus-Minuartia groenlandica* type *Juncus trifidus* is an amphi-Atlantic "Area-geographical differential species"; and a low arctic-oceanic "Climatic indicator," and as an "Ecogeographical guiding species" an oxylophyte climatically adapted to withstand areas bare of snow and exposed to wind. *Luzula spicata* is low arctic, slightly oceanic, amphi-Atlantic-North Pacific oxylophyte which may also occur on almost neutral soil.

Böcher distinguishes and characterizes five climatic types in Southwest Greenland; the low arctic-oceanic, low arctic-suboceanic, low arctic-subarctic continental, low arctic subcontinental, and subarctic oceanic-suboceanic.

The numerous community-types are grouped and discussed in detail in two main categories; an oceanic and a continental vegetation region. Many tables, dot distribution maps, and photographs supplement the text. In addition the vegetation is classified in a synopsis into groups on the basis of physiognonmy and life-form (pp. 307-309). In the appendix a new species (*Synedra subrhombica* Nygaard) and two new varieties of diatoms are described.

An extensive bibliography and indices complete the volume. While the use of the groups of characterizing species is cumbersome, this carefully prepared publication is a mine of information about the vegetation of Southwest Greenland. It represents a distinctive approach to analysis and classification of plant communities through distributional relations of their species. Many communities that are described have counterparts in Alaska and in Scandinavia, and so it should be of great value in the study of arctic and subarctic vegetation in both North America and Eurasia.

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[1] Böcher, Tyge W. 1954. Oceanic and continental vegetational complexes in Southwest Greenland. Meddelelser om Grønland, bd. 148. Nr. 1: 1-336. 74 figs., 4 plates. Danish Kr. 50.00, $7.25.

PRACTICAL PLANT ECOLOGY[1]

This is the second (revised) edition of a book originally published in 1950. It is intended as a practical guide to the study of plant ecology and is specially prepared for the forest and prairie vegetation which occurs in the region around Wisconsin.

It is printed on one side of the paper only. A brief introduction outlines the scope of the book which is divided into three sections: exercises, reference materials and literature references.

The section on laboratory and field exercises (47 pp.) consists of twelve exercises. In each is given a brief account of the theory lying behind the practical work, details of methods for the various exercises, perforated charts for recording data, literature references and a list of plant material and laboratory equipment required. Laboratory exercises come first and deal with the adaptation of plants to water, plant competition and the effect of shade on plant form. An exercise on the methods of measurement of some environmental factors is followed by the field exercises. There are four exercises on quantitative ecology (called community life) dealing with the use of quadrats, quarters, transects and the analysis of the spatial distribution of plant individuals. Maps of the distribution of species in three types of vegetation are provided so that the students can sample these in the laboratory before proceeding into the field. Finally, there are exercises on pollen analysis, weeds in a secondary succession, and the effects of fire and grazing on vegetation.

The section on reference materials (30 pp.) consists of three parts. First, there are keys, based on vegetative features, to the following plant groups: timbers (called stump woods), trees and shrubs in winter and in summer, and grasses. These keys are designed only for the species occurring in southern Wisconsin, i.e. the ones likely to be encountered on local field trips. Secondly, there are maps of the vegetation of the United States and of the vegetation and soils of the North Central United States. Thirdly, there are four conversion tables for the determination of humidity and basal area.

The literature references (9 pp.) are designed to fit the author's lectures and are grouped under various headings.

This book is designed for students of Wisconsin University and its value to other students will be small. The exercises in this book do not seem well balanced. Ecological anatomy and physiological ecology are briefly dealt with. Either their treatment should be fuller or they should be reserved for the anatomy and physiology courses. There are no exercises on surveying methods. The exercise on soil methods only includes soil moisture, water retaining capacity and acidity, for which is described the unsatisfactory colourimetric method.

The exercises on quantitative ecology are detailed, though the description of the transect method in Exercise 7 may confuse students as to the nature of a transect. The line transect or intercept method is undoubtedly useful for the analysis of vegetation which is mainly composed of species which do not consist of discrete individuals, but a transect is primarily intended to analyse transitions between vegetation types. It should also be emphasised that sampling the vegetation on population maps (the field data sheets in the rear pocket of the book) is no substitute for work in the field and that the value of their use at all is open to question. The exercise on determining the spatial distribution of plant individuals makes use of Whitford's Index of Aggregation, which is simple to use but of uncertain value. The reliable methods are more involved and it is probably best to reserve the study of spatial distribution for more advanced students.

The keys will be of use to students unfamiliar with the species but the use of common names is to be deplored. The references are almost wholly restricted to works in English and mainly refer to the vegetation of America and hence cannot be a truly representative sample.

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[1] Curtis, J. T. 1956. Plant ecology workbook: laboratory, field and reference manual. Revised edition 1956. Minneapolis: Burgess Publ. Co. iii + 86 pp., figs. and 4 tables. $3.25.

LIFE FORMS OF FOSSIL PLANTS[1]

Some years ago the author of this book submitted for publication a larger work on the same subject. The refusal of its publication stimulated the writing of this present book which the author concludes with the following sentence: "In now appealing to my brother botanists against this verdict I would at the same time be glad to hear whether Messrs. K. Jessen and Ø. Winge or the present author must be supposed to have judged rightly in this matter."

The reviewer of this book is hence set up as a judge. This is an impossible situation as only the present book can be reviewed, and not the original larger unpublished work. If the present book is a summarized form of the original, and if its arguments are convincing, then there is a high probability that the arguments of the original will also be convincing.

From the analysis of the fossil record of flowering plants as obtained from the literature, tables have been prepared showing the number of species in geological periods, life-forms, and Köppen's climatic regions. From these tables it is concluded that the Megaphanerophytes and Mesophanerophytes were the earliest life forms to evolve and that the most recent ones are the Chamaephytes, Geophytes and Therophytes. The evidence from plant geography is used as a secondary support to this argument.

The determination of the life form of a fossil species which has living representatives is easy. When a species had no living representatives its life form was taken to be the same as that of its nearest living relative. This is an unsatisfactory method liable to lead to great errors.

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[1] Hansen, H. Mølholm. 1956. Life forms as age indicators. Ringkjøbing: A. Rasmussens Bogtrykkeri. 50 pp., 18 tables.

The classification of plant life forms is based on the position of the persisting bud during the unfavourable season. This must be extremely difficult to determine with any accuracy for fossil species. It is a pity that this point is not expounded more fully.

As the process of fossilization is highly selective, the fossil record is not a random sample of the species existing at a particular geological time. Thus the life forms of fossil plants are not an adequate representative sample of the life forms occurring in a particular geological period, and great care must be taken in any argument based on them. This difficulty is not mentioned in the present work.

The tables contain some numbers printed in bold type: the significance of this is not explained. Latin names are given without being in italics. There are no references and no acknowledgments.

The author appears to have had two difficulties. First, any condensation of a large work into a very much smaller one is never really satisfactory. Secondly, his style of writing, probably due to writing in a foreign language, makes reading difficult. Errors such as the word "by" instead of "from" on line 22 of page 13 are too frequent for their cause to be inefficient proofreading. It seems a pity that the author did not have his manuscript revised by someone more acquainted with the English language.

These two difficulties may explain some of the incoherencies in the argument presented. Nevertheless the impression left is that the author himself was not really sure what he was trying to say. This reviewer is inclined to support the verdict of Jessen and Winge.

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TROPICAL SOILS[1]

Should an ecologist read this book? By all means. It provides a welcome supplement to many American texts in soil science which are dominated by agricultural outlooks and which are written for freshmen and sophomores. TROPICAL SOILS stresses the origin of soils. It is a meaty dish for graduate students and research workers. Its study requires concentration, but the effort is rewarding.

The real scope of the book is revealed in the subtitle: "A critical study of soil genesis as related to climate, rock and vegetation," a subject matter very attractive to ecologists. Further insight is gained from the sixteen chapter headings. Here is a selection: fundamental considerations of atmospheric climate and soil climate; climate versus rock in tropical soil formation; rock weathering; clay mineral formation in tropical soils; factors governing the formation and decomposition of organic matter; genetic conceptions of tropical soil formation; lateritic soils; podsolic soils; etc.

No book will satisfy everybody. This reviewer, who is interested in soil-forming factors and system analysis, is surprised at the logical inconsistency and nonchalance which often permeates the analysis of interactions of soil, vegetation, and environment. The authors repeatedly shift the frame of reference, from ecosystem, to soil, to part of a soil. Each shift implies a new definition of "environment." Unless this is explicitly recognized the discussion easily assumes ambiguity.

The two authors, Mohr and Van Baren, are well-known Dutch pedologists who have had many years of experience in the former Dutch East Indies. They do not give a neutral "objective treatise"; rather, they freely express their personal opinions, likes and dislikes—which, in the reviewer's opinion, is a stimulating approach. At times it becomes tiresome. For instance, they spare no pains to repeatedly tell the people who operate with air climate how ignorant they are, that soil climate is the crucial thing, etc. But, when the chips are down, the authors correlate soil properties with atmospheric climate, like everybody else.

Very valuable are the detailed discussions of the processes of soil formation, the considerations of gains and losses of elements, the interpretations of chemical analyses, the mineralogical assays, and particularly the survey and digest of tropical clay research. These portions are a rich storehouse of information and ideas. Nothing comparable exists in the English literature. As a matter of fact, probably few people can match the authors' combined knowledge of field and laboratory research.

One misses an evaluation of Kubiena's significant work on rubification and laterization. References to American workers are sketchy. From the standpoint of regional soil science the title of the book is too inclusive, as the authors speak with authority only about the Indonesian Archipelago; but in that area, their authority is impressive.

Printing is first class, done in the Netherlands. There are over one-hundred figures and photographs, all instructive and beautiful. Several color plates enrich the volume. TROPICAL SOILS is highly recommended to students of soils and related fields.

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[1] Mohr, E. C. J. and F. A. van Baren. 1954. Tropical soils: A critical study of soil genesis as related to climate, rock and vegetation. The Hague and Bandung: W. van Hoeve; London and New York: Interscience Publishers, Inc. 498 pp., 103 figs., 4 color plates, 143 tables. $9.00.

NORTHERN CONIFEROUS FOREST SOILS[1]

This is an English version of NORDSVENSKA SKOGSMARKEN (1940), a book written at the request of, and published by, the Swedish Norrland forestry society. It surveys the bases of productivity in Swedish coniferous forest soils. As the British translator notes, "Concerning the subject of forest soil science, as well as other aspects of forestry, we have still much to learn from workers abroad and, until we have made considerably greater progress ourselves, it would appear to be desirable to benefit from what others have done and to use the best available works as a basis on which to build." For the new edition, Prof. Tamm has included some post-1940 research results, plus a chapter on peat soils.

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[1] Tamm, Olov. 1950. Northern coniferous forest soils. A popular survey of the phenomena which determine the productive character of the forest soils of North Sweden. Translated from the Swedish by Mark L. Anderson. Oxford: The Scrivener Press. xi + 253 pp., 21 figs., 19 tables. Available from the Department of Forestry, University of Edinburgh, 10 George Square, Edinburgh 8, Scotland. $3.20.

Particularly for northern American forestry, this book has application. If one has it in Alaska, he can find illustrations on every hand to match those in the book. Two quirks make it less useful. One is the almost complete conversion of Tamm's metric system of units to English units. The clumsiness of the latter needs no further elaboration. Secondly, the Swedish vernacular names of plants are given as English names, most of which are strange to Americans. One *can* find the scientific name of the plant being considered using Gray's Manual, for example.

For ecologists the book contains much of interest. Chapters on the general ecology of coniferous forests, the forest plant associations of northern Sweden, climate, and, after ten chapters specifically on forest soils, the occurrence and development of northern Swedish forest plant associations are excellent ecology. They are firmly based in plant sociology. Two final chapters sum up ideas on soil productivity and its permanence and aspects of practical forest soil classification. Tamm believes the first objective of forest soil science is to distinguish and classify different kinds of soils; second is the study of their ecology. The analogy with the study of vegetation would seem to be direct. Unfortunately, American forestry in most areas lacks the well-elaborated and extensively tested system of forest types (Cajander's) with which Tamm operates so effectively.

Plant succession is a recurrent theme. According to Tamm, to avoid the use of exclusively circumstantial evidence, succession must be studied over a long period of time on one site. At this site the ecosystem must be defined in terms of soil parent material, soil development, and climate (including local climate and ground water) before plant succession can be profitably discussed. Plant succession takes place within a defined ecoystem. As Tamm uses it, plant succession is an empirical phenomenon; it is not a system of plant ecology. To get down to actual cases, clear-cutting and burning are said to be a natural method of forest regeneration in northern Sweden, although *some* spruce forests have not been burned for centuries. With the progress of plant succession, less desirable forest conditions may develop. It is obviously necessary to have such detailed studies of the actual nature and course of vegetation changes as are known from northern Sweden, if plant succession is to be a useful tool for the forester.

The same necessity applies to Tamm's idea that a disharmony between soil and vegetation indicates a problem to be investigated. Ideas of disharmony in the ecosystem and progressive or retrogressive succession must be culminations of much descriptive ecology, such as Tamm has available. These ideas are impertinent without such work.

Stable forests can be related to particular constellations of permanent site factors such as ground water, low nutrient level of the soil parent material, local climates, etc.; "forests whose stability cannot be proved" show no such invariant relationship. These would seem to be ways to define climax and non-climax plant communities.

On the ecology of soils, as already mentioned, general ecology, plant communities, and climate are described as bases for the soil considerations. The latter include chapters on northern Swedish parent-material mineralogies, geological deposition of parent materials, bedrock geology, organic matter of forest soils, and on soil formation. The latter ties together the information on the soil-forming factors. Then podsol soils are examined systematically and in detail, next soil water, soil heat, mull and mor humus types, and peat soils. The soil is differentiated from geological deposits because it contains organic matter. Throughout, the ecosystem, with its soil, is the focus of interest. An association of plants is the principal biotic part of this ecosystem.

While our American plant associations do differ from the Swedish, in as yet mostly unknown ways, toward our own north differences become less, and in Alaska at least this book would be an excellent text for forest soils. Similarities of conifer forest tree genera, universally leached soils, and the same moss, lichen, ericaceous, and many other herbaceous and shrub species in the ground vegetation, and zonal prevalence of podsols relate the two regions.

Whereas American forest soil work is mostly an outgrowth of agronomy and a soil science often submersed in agriculture, Tamm's is a really natural science. His is an ecological viewpoint. Thus, while soils with high water tables seem to offer the soil physicist few problems, they offer many to plants, and Tamm discusses such soils. Again, morphology of these podsols is a more sensitive indicator of soil processes than are chemical analyses. Besides the standard effects of climate, soil mineralogy, relief, and ground water on soil formation, the effects of vegetation are continuously considered: fire leads to permanent soil impoverishment in some cases; the normal course of podsolic soil development inevitably produces this poorer result also; windthrow mixes profiles; permafrost forms in relation to vegetation changes; swamping is a natural or induced process; flushes related to movement of nutrient-rich ground water are indicated by vegetation; frost-lifting of stones is related to litter cover, etc.

Tamm's book is an excellent distillation of research results and makes available much scattered Scandinavian literature. The few misprints (ferrous, p. 119, "former" instead of "water" p. 130, Chamaenerion p. 192) do not disturb. The book encourages the reader because it means to popularize pedological and associated vegetation knowledge for forestry purposes, and so itself supplies much necessary background. Because the translation is quite literal, the book many have a further value in providing, with the 1940 Swedish edition, parallel texts for those who would like to learn more of a language in which so much excellent ecology has been written.

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MINERAL NUTRITION OF FORESTS[1]

This bibliography of 700 items is intended as an aid for "increasing the growth of forests and bringing waste lands into useful timber production by the use of fertilizers and other soil amendments." It includes a great deal of work on tree nutrition which will be valuable to ecologists. Unfortunately it neglects a few journals, such as the BRITISH JOURNAL OF SOIL SCIENCE, JOURNAL OF ECOLOGY, and NEW PHYTOLOGIST, all of which have printed papers similar to those included.

The ecologist might tend to dismiss this compilation, since he usually thinks of himself as studying plants under natural conditions. As one abstract notes (p. 240), "Particularly in the growing of exotic trees in plantations, the forester is more closely approaching agriculture where use is made of cultivation and artificial fertilizers." However, we are obtaining much evidence that under natural, or at least normal, conditions much forest land is either extremely bad off, or becoming worse, so that it will not support good tree growth. For example, Rennie[2] has concluded that some soils in England simply lack the nutrients to support timber-producing forests. Of great interest to us as we convert virgin to managed forests is Rennie's conclusion that the presence of a fine virgin forest on a site is simply no criterion of that site's ability to sustain a commercial forest. Removal of a forest can expose nutrients to leaching losses rather than to uptake by vegetation. Just this process is blamed by Duchaufour[3] for the irreversible podsolization, leading to site degeneration of the massive ortstein variety, in sandy soils of Atlantic France. These formerly forested soils will now support only heath. In all these cases commercial forestry will have to involve fertilization merely to maintain site quality or to grow forests at all. The necessity of obtaining ecological information before drastic mistakes are made is obvious. For example, liming can lead to loss of K and Mg or unavailability of micronutrients, as it has in agriculture, and these changes can be castastrophic over the long span of time during which a tree crop grows. However, this bibliography makes available much of the knowledge we now have on the uses of fertilizers in forestry, and so it will be valuable in rectifying unfavorable natural conditions of forest growth.

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[1] White, D. P. and A. L. Leaf (compilers). 1957. Forest fertilization. A bibliography, with abstracts, on the use of fertilizers and soil amendments in forestry. Technical Publication 81, College of Forestry, Syracuse University, New York. World Forestry Series Bull. 2. 306 pp.

[2] Rennie, P. J. 1955. The uptake of nutrients by mature forest growth. Plant and Soil 7: 49-95.

[3] Duchaufour, P. 1948. Recherches écologique sur la Chênaie atlantique française. Annales de l'École Nationale des Eaux et Forêts, Nancy. 332 pp.

SOIL[1]

The U. S. Department of Agriculture has for many years devoted the Yearbook of Agriculture to one specific subject. The 1957 Yearbook is concerned primarily with the management of soils. Eight major sections (principles, fertility, practices, soil care, moisture, systems, regions, and special uses) are discussed. The first 80 pages constitute a group of well-written, factual papers dealing primarily with fundamentals and soil principles; and there are few who would fail to profit by reading this section. Sections dealing with fertility, practices, and moisture are considered informative; and nearly all are well written. As to those parts relating to soil care and soil systems, some are worthwhile; but on the other hand, there are a number of papers with some shortcomings. The last two sections dealing with regions and special uses are somewhat dull, and reading these pages is not too rewarding. The first part of the volume is of good quality, but the later part is one of considerable monotony.

Near the end of the book are 20 pages of soils and related definitions that are very helpful. Numerous simplified drawings, sketches and generalized maps are employed throughout the book. There are very few tables.

It is doubtful if this volume will have such impact on the field of soils, biology, and related earth sciences as did its predecessor, the 1938 Yearbook—SOILS AND MEN.

The book can be purchased from the Superintendent of Documents, Washington 25, D. C.; however, a letter to a local U. S. senator or representative usually will bring a free copy.

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[1] Stefferud, Alfred, editor. 1957. Soil: The Yearbook of Agriculture, 1957. (Symposium) Washington: U. S. Dept. Agric., U. S. Gov't Printing Office. xiii + 784 pp., figs. and tables. $2.25.

ECOLOGY OF MICROBES[1]

The field ecologist, studying the synecology of a prairie, desert or forest plant association, the economy of a mammalian population of an offshore island, or the ecosystem of a pond, rarely more than recognizes the existence of organisms not macroscopically observable at the moment, or not readily observable in a plankton counting device. Thus are lost to him the myriads of microorganisms which form part of the plant community, the mammalian population, or the ecosystem under study.

The ecologist, studying the field aspects of the autecology of a tree, an herb, or an animal, does not always observe, realize, or report the effects of the large population of microorganisms associated with the macroorganism as members of a bark, bud or root population or as commensal organisms on the fur, feathers, nails or hooves of the animal, or as parasites in its mouth or internal organs.

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[1] Williams, R. E. O., and C. C. Spicer, editors. 1957. Microbial ecology, Seventh symposium of the Society for General Microbiology. Cambridge and New York: Cambridge University Press. ix + 388 pp., figs. $6.50.

In introducing the symposium, MICROBIAL ECOLOGY, C. J. Shepherd said: "Ecology is the study of the interactions of organisms and environments." One can interpret this definition to refer to all organisms and all environments, or one can restrict it to all organisms in one general environment, several sets of organisms each in its particular phase of one environment, or a single organism in the many phases of the environment in which it exists during the completion of its life history. Following the general tenor of the several papers which compose the symposium, the last type of study would be best for a complete perusal of the ecological life history of a microorganism. Several specific factors in the environment of microorganisms are considered; then particular groups of microorganisms are studied in relation to the action of environment on each, and the effect of each on its environment, its host or on a larger population. It is of interest to note that most of the organisms considered in the symposium are of importance to man, or to the animals and plants grown by man for food. Other groups of organisms are considered because of special interest, or because of an accidental correlation with disease. It is emphasized and reemphasized that in many areas of study which are covered, insufficient data are available to present conclusive arguments.

On the basis of the fact that the genetic constitution of an organism directly affects the organism in relation to its environment, Shepherd redefines ecology as a "study of genome-controlled phenotypes in relation to their environments."

Environment plays a major role in the ecology of microorganisms. Isolation from their natural habitats, whether these are organic materials in process of decay or living organisms under attack by pathogens, is based primarily on selective enrichment media. From this starting point the discovery of optimum nutrient requirements or best enrichment media for primary isolation may be determined. Symbiotic relationships between two species of bacteria in the same culture are considered. The Van Niel modification of the Koch postulates is discussed in relation to recovery of the microorganism from a medium in which a chemical process has taken place. The microbiology of the rumen is discussed at length.

Hydrogen-ion concentration and oxidation-reduction conditions of various types of media and bacterial habitats are important not only in the medium but also in the cytoplasm of the organism. Temperature may play an important role in determining the reaction of bacteria and other microorganisms to conditions of high pressure such as may be found in deep mines and wells and in the depths of the ocean. The phenomena of pressure and their effects on bacteria are described by physical formulae.

Solar radiation plays an important part in the lives and growth conditions of several small groups of microorganisms. In addition to the algae, these include the green and purple bacteria. Some of these organisms are obligate anaerobes; others require oxygen. Many heterotrophic organisms have carotenoid pigments which are important in their life functions. Problems of chemotrophy, autotrophy and heterotrophy are considered.

Two highly specialized groups of microorganisms include bacteria existing under conditions of high salt concentrations such as may be found in the ocean, in the Great Salt Lake, or in saline soils, and those yeasts found in high concentrations of sugar. The various conditions under which such concentrations of salt and sugar can exist in nature and under which they can be tolerated by bacteria and yeasts are explored in considerable detail.

On fragments of organic debris in the soil, on seed coats and in the rhizosphere occur a number of fungi and bacteria which can produce antibiotics under some laboratory conditions. The possibility that such substances may be produced in nature is considered in detail and the decision is reached that they can be so produced under special conditions. A new technique is described for the study of the natural occurrence in the soil of cellulose-decomposing fungi. On the basis of the use of cellulose film as a colonizing medium, new concepts have been developed concerning the occurrence and distribution of such fungi in the soil.

It has been shown in the medical laboratory that bacteriophages are of importance to the ecology of bacteria. Evidence of the incidence of phages in sewage and faeces, and of the growth of phages in sewage, are treated in some detail. The latter work is based largely on several species of *Salmonella* phages. In addition to attacking bacteria, viruses attack higher plants, animals and man. They appear to have a distinct ecology, and problems of myxomatosis of rabbits, influenza of man and other diseases caused by viruses are discussed in relation to the four principal "activities" of viruses: "getting in" or contact with the host and entry into it, multiplcation, "getting out" or dispersal from the host, and "getting about" or survival outside the host.

One of the important problems in the distribution of plant viruses is the knowledge of which virus is carried by which insect vector. In some cases there is mechanical transmission, without insect intervention; in others mandibulate insects are known to transmit the viruses. Primarily the ecology of plant viruses is strongly tied to the ecology of sucking insects such as aphids, and the ability of viruses to multiply within the insect vector.

Fungi have a number of ways of surviving adverse conditions. Such methods as the development of specialized vegetative cells, sclerotia, rhizomorphs, spores and fruit bodies are considered. By rapid spread a fungus can escape an unfavorable environment, or it can colonize a borderline habitat in which, during one part of its life history, it can utilize one source of nutrient, later another. Among the more interesting of the latter types are those capable of trapping or ensnaring nematodes and other microscopic animals. Techniques of predation, biotic control of nematodes which cause serious crop losses, and other factors concerning the ecology of these fungi have been intensively studied in England and the United States.

Supplementary reading on the chapter "Ecological factors and the survival of fungi" in which one gains further insight into the reproduction of fungi from the physiological point of view can be had by reading a recent book by Hawker.[2] This small volume considers such subjects as growth of spores and spore-bearing structures, physiology of vegetative reproduction, effects of environment and nutrition on sporulation, physiology of sex and loss of sexuality, and reproduction in the natural habitat.

Free-living protozoa are brought into the general perspective of MICROBIAL ECOLOGY by a description of their habitats, patterns of biological response such as cultural growth, predator-prey populations, competitions, and the factors involved in cyst formation. Effects of temperature, salinity, oxygen, pH, carbon dioxide concentration, and tidal rhythms are also considered.

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[2] Hawker, L. E. 1957. The physiology of reproduction in fungi. Cambridge and New York: Cambridge University Press. viii + 128 pp. $3.00.

Problems of bacterial ecology seem at present to be largely confined to the study of the relation between bacteria pathogenic for man and their host. The complex interactions between man and those bacteria which cause disease in both himself and his domesticated animals are considered on the basis of altering the microbial ecology by attempts to control their pathogenic activities. Epidemiological aspects of this problem are considered from the point of view of the effect on bacterial virulence of the selective action of various factors inside and outside the human or animal body.

Plant hosts have a marked effect on their populations whether the microorganisms are pathogens, members of the rhizosphere or of surrounding soils. The general effect on the environment and on the microbial population is considered when a native plant population is replaced by an introduced cultivated crop of thousands of plants of the same host species. F. C. Bawden states that ". . . the interactions between hosts and parasites are so varied that every ecological situation is best considered as though it were unique."

In general, where fields of endeavor overlap, considerable harmony between workers is expressed or implied in the chapters of this volume. However, an undercurrent of controversy is implied in the discussions of fungi, especially of those implicated in root disease problems. Some of Bawden's statements contrast sharply with ideas expressed by Garrett in work reviewed earlier and mentioned by Brian and Hawker in this volume.

Correlative reading in microbial ecology should include the volume on ADAPTATION IN MICROORGANISMS.[3] It must be repeated that because of the ease with which such organisms can be handled in the laboratory, their relatively short generation period, and their importance to man either from the point of view of pathogenicity or productiveness, they have been used extensively in laboratory experimentation. Here evolutionary and physiological adaptation can be studied easily. Genetic and cytoplasmic mutation can be compared with enzymic adaptation which can be manipulated in numerous ways. Products of the biosynthesis of antibiotics on a large scale can lead to additional enzymatic changes in the metabolism of the organism whose control is being sought. These changes may negate such control and at the same time intensify the search for antibiotic producers. Specialized adaptations are considered for antibiotic resistance and for effects of bacteriophages on their hosts. Various types of adaptations are considered for *Paramecium,* thermophilic organisms, and fungi.

If we translate the activities discussed in the later part of the Seventh Symposium in terms of the physiological and genetic concepts outlined in the earlier papers and in the Third Symposium, we may agree with F. H. Johnson who says: "While the ultimate goal of ecology—interpretation of all interrelationships in terms of the structure and behaviour of molecules—is still only a faint smudge on a distant horizon, the progress of modern physics, chemistry and biology contains an encouraging hint of eventual success."

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[3] Davies, R., and E. F. Gale, editors. 1953. Adaptation in microorganisms, Third symposium of the Society for General Microbiology. Cambridge and New York: Cambridge University Press. ix + 339 pp., figs. $6.00.